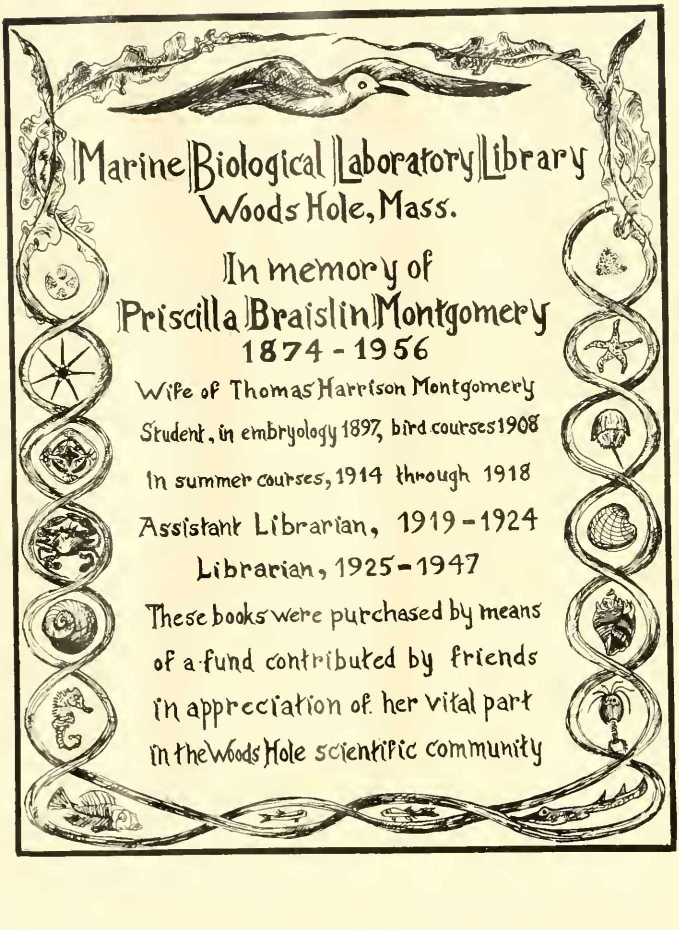
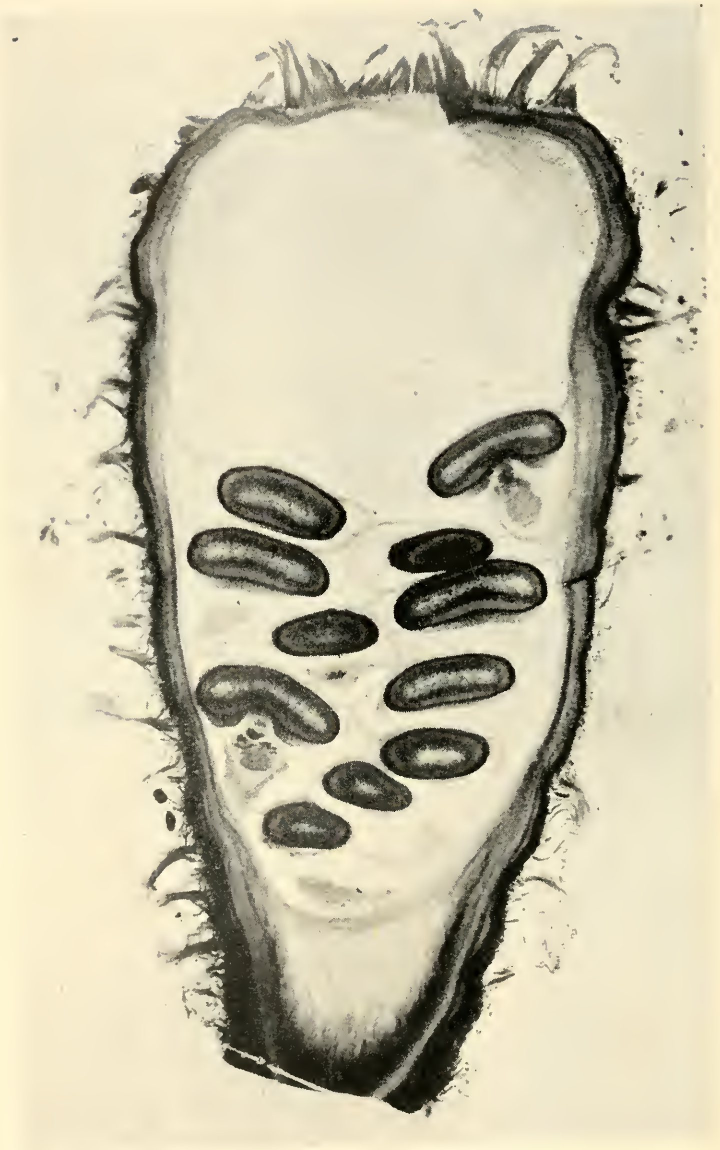


TEXTBOOK OF THEORETICAL BOTANY



Cyathus striatus. Longitudinal section through a mature fruiting body showing the epiphragm closing the apex, and developing peridiola enclosed by the peridium.

TEXTBOOK OF
THEORETICAL
BOTANY

BY

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VOLUME I

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PREFACE

The attempt to write a textbook of Botany is an audacity which admits of no excuse but success. Botany is the *scientia scientiarum*, and it draws its inspiration from many worlds. On the one hand, it is a modern experimental discipline ; on the other hand, it is a storehouse of curious and ancient lore.

Botany has fortunately retained its historical unity of purpose, despite the vast modern extension of knowledge and the concurrent growth of specialism. It sets out to comprehend the plant from every point of view, and it has not yet ceded any of its territory to others, though some of its numerous daughter sciences seem to be growing quickly towards independence and claiming a position as heirs of their venerable parent. Few other subjects in the calendar of the sciences present so varied a catalogue of interests, and probably none of them stands in greater need of condensation into assimilable form.

There exist already many admirable treatises by specialists, covering separate sections of the field, which are of the utmost value to those who are specialists themselves, but which are for the most part beyond the range of the general student. There are also many valuable elementary surveys, which hardly go further than the first year of university study. The present work aims to fill the gap between these extremes, and its bulk is sufficient evidence that the gap is considerable.

We have drawn freely from many specialized sources, but the various sections of the book are not written for specialists. We hope that it will not be judged as if it were a collection of monographs bound together, but rather as a general text for general students in which unity and clarity are not subordinated to the elaboration of unessential detail. Indeed every endeavour has been made to exclude detail which does not contribute in some measure to the composition of the whole picture.

In dealing with the groups of lower plants we have adopted the type method, which is in some danger of being considered old-fashioned. Experience has led us, however, to believe that the method is still sound and useful. A detailed description has been given of at least one species in each major group, selected because it is well known, fully investigated, and really representative of its group. The descriptions given have been in all cases checked and amplified by reference to all the sources of information available, including the results of recent research, and we hope that they will stand scrutiny. These descriptions we regard as foundations on which may be built a further study of the group. Our contention is that if a student masters the particulars of structure and life-history in the selected type the related forms will fall naturally into place in their proper perspective. A clearer appreciation of the characteristics of the group as a whole is to be obtained in this way than by the compilation of scraps of information treated comparatively, which gives no coherent account of any one organism in full.

Based on such a principle this work can obviously make no claim to be a textbook of comparative morphology. The presentation of comparative accounts and the deduction of relationships and of phylogeny we regard as the special function of the lecturer. University lecturing should certainly not, in any case, be devoted to the kind of factual material which it should be the function of a textbook to convey. To place such material in the hands of the student in book form is to free the lecturer to perform his true function, namely to review his subject in the light of his personal knowledge.

Theoretical problems are not, of course, wholly ruled out of discussion in our descriptions, though they tend to become more prominent in the later chapters than in the strict treatment of types. Above the Gymnosperms, typology becomes impracticable, and in the non-morphological branches, such as Physiology, Ecology and Genetics, theoretical discussions are naturally the order of the day. We have tried in such matters to avoid dogmatism, and we have only occasionally ventured to hint at our own opinions, so that these discussions are also largely factual in the sense that they are presentations of ideas and interpretations which have been formerly advanced or which are actually current.

Among the general subjects treated we have laid some emphasis on Economic Botany, to which a chapter is devoted. Not many schools of Botany include this subject in their undergraduate courses, but we feel that the omission is one which must soon be remedied. We hope that the day of those who sneered at " merely useful knowledge " has gone by, and the great service which plant science renders to the welfare of mankind will no longer be ignored by scientists under the specious plea of purity, which is so often no more than a wilful blindness to the world around.

The chapter of Bionomics also demands a word of notice. The word is not familiar in modern textbooks, but it is an expressive and useful term with which to describe the series of phenomena which, for want of a better name, we can call adaptations. In the widest sense the subject-matter is ecological and must be ecologically viewed, but it is sufficiently distinct to be worthy of separate treatment, apart from the fact that its inclusion under Ecology would have swollen that chapter unduly.

Palaeobotany, likewise, has been discussed separately. In comparative courses this would not normally be done, but the type system does not lend itself to expressing the relationships of plants of different groups, and we feel that a survey of fossil plants stratigraphically, as a series of successive floras, has a value of its own, and may also be helpful in comparative studies.

We were ambitious to make the text sufficiently well illustrated to compare favourably in this respect with the German texts which have dominated European science for two generations. They owed their great popularity not least to their wealth of illustrations. The present time is propitious for establishing in other countries the claims of British scientific publications, and we hope that this effort will not be in vain. A very large number of the illustrations are photographs from original material, even in cases where well-known figures were already available. The naturalistic quality of photographs needs no emphasis, and they may afford a pleasing variation from well-known figures which custom has rendered stale.

The theoretical textbook will appear in four volumes. The arrangement of the chapters follows the evolutionary sequence of treatment, and it is hoped that for this reason students will be able to work with one volume at a time, and therefore save the heavy cost of buying all four volumes simultaneously.

Messrs Longmans, Green and Co. are about to publish as a companion work to the present book, a " Textbook of Practical Botany," which we have compiled as a laboratory guide for practical studies. The plan of the book follows the same lines as the present theoretical work. The experimental sections on Physiology, Ecology, Genetics, etc., are designed to illustrate the theoretical concepts discussed in the later volumes of the present work, while in Morphology the same elementary types which are described here are also treated in the practical book. Only the types intended for more advanced students have been omitted, partly because such practical directions at the advanced level should be largely superfluous, and partly because the material available in the laboratory may change from year to year.

Students who are commencing a study of Botany, and who are using this theoretical textbook, will find the practical book a great help. It is, moreover, because of the existence of this practical work that experimental details and instructions in laboratory technique generally have been entirely omitted from the present volumes. It is hoped that the " Textbook of Practical Botany " will appear shortly after the publication of Volume I. of the " Textbook of Theoretical Botany."

We hope that it may be possible for students to use this book from the beginning of their studies onwards, throughout their degree courses.

Elementary types have been specially treated, all the essentials being marked in heavy type, so as to make them easy to follow, even for the beginner, while in each general section a statement of elementary points has been included, on which the beginner may concentrate his attention, leaving the fuller treatment for later study. We emphasize this because we do not wish the impression to prevail that a textbook as large as this must necessarily be far beyond the needs or the grasp of the first-year student. No doubt much of it is beyond him, but we believe that the above provisions for his requirements may make it possible to use the book at all stages, with the advantages which may thus be gained from thorough familiarity with one comprehensive source during several years.

On one important question we feel obliged to state our opinion, the question, namely, of the use of teleological expressions in describing the life-processes of the plant.

The natural reaction against the crude teleology of the adaptationists has been carried to extravagant lengths, and has become a pedantic insistence on purely mechanistic terminology, which amounts to a sedulous pretence that the plant is not alive. Such fictional concepts have their undoubted uses, so long as we do not forget that they are simply constructional fictions. The living organism is no doubt a physico-chemical mechanism, and it may be to some extent analysed in such terms, but to insist that it can be completely expressed as a test-tube filled with reactant substances is definitely unscientific. It implies the rejection, *a priori*, of a whole category of phenomena which are not covered by such a theory, but which are just as much facts as are the chemical reactions, and are indeed those very phenomena which give Biology its validity as a separate science. The existence of purpose in our own nature is practically the only phenomenon of which we have immediate perception, and it is highly irrational to exclude it from all the rest of the universe. We need not use it in our accounts of the construction of a living mechanism, but we must use it in considering the operation of the mechanism or the universe becomes meaningless. It may perhaps be an act of presumption to believe that a living organism can ever be fully understood, but we warn the reader that in our efforts towards this goal we shall employ the word " function," with all that it implies, when we think it is needed, and we shall do so on principle and not merely to avoid tiresome periphrasis.

Botany has moved far since 1829, when Loudon wrote that " the Science of Botany consists of two departments : Phytology and Physiology." The botanical scene has changed many times in the intervening century, and it becomes daily more difficult, as our periodicals show us, to say what is Botany and what is not. In order to cover the subject adequately we have not quite, in Chestertonian phrase, to get the heavens into our head, but nevertheless the task of compression is difficult enough. For the imperfections of what we have accomplished in this way, we can only ask for the kindly indulgence of those who from their specialist knowledge could without doubt have written their own particular sections very much better. It was because we felt that the work should be a balanced survey that we attempted to write the whole of it ourselves.

We wish to thank our publishers for allowing us to illustrate the text so fully. The illustrations consist largely of photographs, most of which we have taken ourselves from material in our own collections or from those of the Department of Botany. A certain number have been obtained through the kindness of friends or from commercial firms, acknowledgment of which is made where they are reproduced. Some illustrations from " Biology for Medical Students," by C. C. Hentschel and W. R. Ivimey-Cook, published by Messrs Longmans, Green and Co., have also been incorporated.

We have also received help in other directions, notably from Professor R. J. Tabor, to whom we owe some very valuable criticisms and suggestions. Lastly we wish to thank Mrs Ivimey-Cook for extensive help in typing and proof correcting, and Mrs McLean for the compilation of the Index, both laborious tasks which were cheerfully undertaken.

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W. R. IVIMEY-COOK.

The University of Wales,
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CONTENTS

GLOSSARY OF PREFIXES AND SUFFIXES

The following list of the more important Greek and Latin roots used in botanical terminology has been compiled to enable the student to understand the meaning of technical terms. With its aid most of those occurring in the text can be readily translated. They are arranged as prefixes and suffixes according to their usual employment, though some may occur in either position. Their derivation from Greek (G.) or Latin (L.) has been indicated in each case.

PREFIXES

a-	not, without (G.).
ab-	from (L.).
acro-	apex (G.).
actino-	radial (G.).
ad-	to, towards (L.).
amphi-	around (G.).
ana-	up (G.).
andro-	male (G.).
anemo-	wind (G.).
angio-	vessel (G.).
angusti-	narrow (L.)
aniso-	unequal (G.).
ante-	before (L.).
anti-	against (G.).
apo-	away from (G.).
arch-	primitive (G.).
asco-	sac (G.).
auto-	self (G.).
aux-	growth (G.).
basid-	pedestal (L.).
bi-	twice (L.).
bio-	life (G.).
botan-	herb (G.).
brachy-	short (G.).
bryo-	moss (G.).
carp-	fruit (G.).
caul-	stem (L.).
chaet-	bristle (G.).
chlamyd-	cloak (G.).
chloro-	green (G.).
chondro-	grainlike (G.).
chromo-	colour (G.).
chryso-	golden (G.).
circum-	around (L.).
co-, *con-*	together (L.).
coeno-	in common (G.).
coleo-	sheath (G.).
crypto-	hidden (G.).
cyano-	blue (G.).
cyto-	cell (G.).

derm-	skin (G.).
desm-	bond (G.).
di-	twice (G.).
dia-	through (G.).
dicho-	separate (G.).
dictyo-	net (G.).
diplo-	double (G.).
dys-	bad (G.).
e-	without (L.).
ecto-	outside (G.).
endo-	inside (G.).
entomo-	insect (G.).
epi-	upon (G.).
erythr-	red (G.).
eu-	well, proper (G.).
eury-	broad (G.).
ex-	out of (L.).
gam-	marriage (G.).
gamet-	spouse (G.).
gastero-	stomach (G.).
ge-	earth (G.).
geitono-	neighbouring (G.).
geno-	racial (G.).
gluc-, *glyc-*	sweet (G.).
goni-	offspring (G.).
gymno-	naked (G.).
gyn-	female (G.).
hadro-	strong (G.).
halo-	salt (G.).
haplo-	single (G.).
helo-	marsh (G.).
helio-	sun (G.).
hemi-	half (G.).
hetero-	different (G.).
hexa-	six (G.).
holo-	entire (G.).
homo-, *homoio-*	alike (G.).
hyalo-	crystal (G.).
hydro-	water (G.).
hyper-	above (G.).
hyph-	web (G.).
hypo-	below (G.).

idio-	peculiar (G.).
infra-, infer-	below (L.).
inter-	between (L.).
intra-	within (L.).
iso-	equal (G.).
karyo- (caryo-)	nut, nucleus (G.).
kata-	down (G.).
lati-	broad (L.).
leuco-	white (G.).
limno-	lake (G.).
lyco-	wolf (G.).
lys-	loosen (G.).
macro-	large, long (G.).
mega-	large (G.).
meio-	less (G.).
melan-	black (G.).
meris-	part (G.).
meso-	middle (G.).
meta-	with (G.).
micro-	small (G.).
mito-	thread (G.).
mon-	single (G.).
morph-	shape (G.).
multi-	many (L.).
myco-	fungus (G.).
myrmeco-	ant (G.).
nan-, nann-	dwarf (G.).
necro-	dead (G.).
neo-	new (G.).
nerit-	coastal (G.).
notho-	false (G.).
nuta-	nodding (L.).
nycti-	night (G.).
ob-	inverse (L.).
oligo-	few (G.).
omni-	all (L.).
oo-, ovo-	egg (G.), (L.).
ornitho-	bird (G.).
ortho-	straight (G.).
oxy-	sharp (G.).
pachy-	thick (G.).
palaeo-	ancient (G.).
pan-	all (G.).
para-	beside (G.).
partheno-	produced without sex (G.).
pelagi-	oceanic (G.).
penta-	five (G.).
peri-	around (G.).
phaeo-	brown (G.).
phanero-	manifest (G.).
pheno-	appearance (G.).

phloe-	bark (G.).
photo-	light (G.).
phyco-	algal (G.).
phylo-	tribe (G.).
physo-	bladder (G.).
pinna-	feather (L.).
plano-	wandering (G.).
pleio-	more (G.).
pluri-	several (L.).
poly-	many (G.).
post-	after (L.).
pre-, prae-	before (L.).
pro-	for (L.).
proto-	first (G.).
pseudo-	false (G.).
psilo-	bare (G.).
ptero-	wing (G.).
quadri-	four (L.).
quater-	fourth (L.).
quinque-	five (L.).
rhiz-	root (G.).
rhodo-	red (G.).
sapro-	putrid (G.).
schizo-	splitting (G.).
scler-	hard (G.).
semi-	half (L.).
siphon-	tube (G.).
solen-	tube (G.).
soma-	body (G.).
sperma-	seed (G.).
sphaero-	spherical (G.).
spheno-	wedge (G.).
squam-	scale (L.).
steno-	narrow (G.).
stereo-	solid (G.).
styl-	column (G.).
sub-	below (L.).
super-, supra-	above (L.).
sym-, syn-, sys-	together (G.).
telo-	end (G.).
ter-	third (L.).
tetra-	four (G.).
thalasso-	marine (G.).
thallo-	sprout (G.).
therm-	heat (G.).
thero-	summer (G.).
trans-	across (L.).
tri-	three (L.), (G.).
tricho-	hair (G.).
uni-	one (L.).
vas-	vessel (L.).
xantho-	yellow (G.).
xeno-	stranger (G.).

xero-	dry (G.).
xyl-	wood (G.).
zoo-	animal (G.).
zygo-	joined (G.).

SUFFIXES

-androus	male (G.).
-angium	vessel (G.).
-arch	beginning (G.).
-blast	bud, rudiment (G.).
-bolic	thrown (G.).
-carp	fruit (G.).
-chasium	separation (G.).
-colous	inhabiting (L.).
-cyclic	circled (G.).
-cyst	cavity (G.).
-cyte	cell (G.).
-dendron	tree (G.).
-derm	skin (G.).
-dynamous	powered (G.).
-enchyma	infusion (G.).
-ferous	bearing (L.).
-fid	cleft (L.).
-folium	leaf (L.).
-fuge	avoiding (L.).
-gen	producing (G.).
-generous	bearing (L.).
-graphic	writing (G.).
-gynous	female (G.).
-kinesis	movement (G.).
-lith	stone (G.).
-logy	knowledge (G.).
-lytic	dissolving (G.).
-merous, -mery	part (G.).
-meter	measure (G.).
-morphic	shaped (G.).
-nastic	pressed (G.).
-nate	born (L.).
-nym	name (G.).
-oecium	dwelling (G.).
-oid	like (G.).
-ont	being (G.).
-phage	eating (G.).
-petal	seeking (L.).
-philous	loving (G.).
-phobic	hating (G.).
-phore	bearer (G.).
-phyll	leaf (G.).
-phyte	plant (G.).
-plasm, -plast	moulded (G.).
-plicate	folded (L.).
-podium	foot (G.).
-rhiza	root (G.).
-scopic	looking (G.).
-sect	cut (L.).
-some, -soma	body (G.).
-sperm	seed (G.).
-spore	germ (G.).
-stachys	spike (G.).
-stele	pillar (G.).
-stichous	ranked (G.).
-tactic	arranged (G.).
-taxis, -taxy	order (G.).
-thallic	shoot (G.).
-theca	case (G.).
-tome, -tomy	cutting (G.).
-tonic	tuning (G.).
-trichous	hairy (G.).
-trophic	nourished (G.).
-tropic	turned (G.).
-ula, -ule	diminutive (G.).
-vorous	consuming (L.).
-zoid	animal-like (G.).

CHAPTER I

INTRODUCTION

When we speak of the Science of Botany to the ordinary man or woman the idea which usually arises in the mind is that of the study of flowers, and as a natural result Botany is conceived by the uninitiated as a science dealing with garden and wayside plants, and the student of Botany as a kind of glorified gardener who knows the proper names of plants and how to grow them. Such a conception is, of course, entirely wrong. Botany is something very much wider than that, for the study of garden flowers is the province of the horticulturist, who may, or may not, be a botanist. Again the knowledge of the names of wild plants is the special work of a small section of botanists, and is not by any means the whole subject.

Natural Science may be divided into the Pure Sciences and the Applied Sciences, the former being concerned with the science of the world in which we live, the latter with the economic and practical applications in which the natural sciences can be employed. The four primary natural sciences are Biology, Geology, Chemistry and Physics. Biology is the science which studies life in all its aspects. Its scope is vast, for it includes not only the study of animals and plants but that of man as well. For practical convenience Biology is divisible into the study of animals and the study of plants. The former we designate as Zoology, the latter as Botany.

Botany, therefore, is the study of life as found in the plant kingdom. In order to appreciate the vast size of this problem, we should realize in the first place that the Flowering Plants only form quite a small proportion of the types of plants known to exist at the present time. Included in the term plants are, of course, the Club Mosses, the Ferns, the Mosses and the Seaweeds, and also a very large assemblage of organisms much less obviously plants, such as the Fungi and Bacteria, and countless different kinds of microscopic organisms which float about in the waters of any pool or stream. Our subject, however, does not end there, for we know from a study of the rocks that many kinds of ancient plants, unlike those of the present day, can be discovered buried in the various geological strata, and a special branch of Botany, **Palaeobotany,** deals exclusively with this section of plants.

Having thus, in very general terms, indicated the range of organisms which are included in the plant kingdom, let us consider the ways in which they may be studied. We may in the first place consider their external form, or we may investigate their internal structure. Thus at the outset we come up against two of the main divisions of the subject, **Morphology** and **Anatomy,** which are themselves closely related to the study of plant evolution or **Phylogeny.** There are many others : the study of the functions of plants is termed **Physiology,** to which may be added the study of the chemistry of plant life, **Biochemistry** ; then there is the study of their development, **Embryology** ; the study of classification, **Taxonomy** ; and the study of inheritance, **Genetics.** We may investigate their mode of living, **Bionomics,** or the relationship between the plant and its habitat, **Ecology.** Then, again, the investigation of certain groups of plants has become frequently a separate sub-science, and we speak of the study of seaweeds as **Algology** ; of fungi as **Mycology** ; of plant diseases as **Plant Pathology** ; of bacteria as **Bacteriology.** There are also certain economic branches of the subject which are more familiar to the man-in-the-street : **Horticulture,** the study of garden plants ; **Forestry,** the study of trees ; **Agricultural Botany,** the study of crop-plants ; and **Pharmacognosy,** the study of drug-plants ; all of which form part of **Economic Botany.**

This, then, may be said to be an outline of the general scope of the science of Botany, which is certainly very different from the popular conception. Moreover, it is important to realize that each of these sub-sciences is dependent upon the others, and that a clear understanding of any one field is impossible without a fundamental knowledge of the essential features of the whole subject. In fact, it is equally true to say that a proper knowledge of Botany cannot be obtained without at the same time gaining an elementary knowledge of the essential features of the whole of Natural Science, that is of the allied sciences of Chemistry, Zoology, Geology and Physics. So dependent are the sciences upon one another, and at the same time so extremely complex has each of them become, that one of the greatest problems which besets a scientist at the present day is how he can become familiar with the details of his own particular section, while, at the same time, remaining acquainted with the current position of the allied branches of science. One of the greatest dangers which we are facing at the present time is the tendency to over-specialization, that is to say, the cultivation of an intensive but exclusive knowledge of a very small part of science with the inevitable result of losing touch with the whole. Such an outlook may advance our knowledge in some particular field of research, but what science needs more than anything else is to be able to take stock of herself, to see whither all modern research is leading, and what advantage, if any, the human race has received in return for all the energy which has been expended. Only by being capable of understanding the fundamental facts in different branches of a science and of various sciences, can such an estimate be made, and it is very important that at the outset of his career a student should attempt to provide himself with the necessary knowledge, for very soon he may be swept up in the train of specialization and fall into danger of losing his sense of proportion.

The Characteristics of Living Organisms

Before commencing our study of Botany it is necessary for us to inquire how we may distinguish living organisms from dead matter ; in other words, how we may limit the territory designated as Biology.

In the present state of scientific knowledge it is impossible to answer the question " What is life ? " though it is possible to describe those characteristics which distinguish the living from the non-living. In living matter we find only those elements which are among the common constituents of the earth, and these elements obey the ordinary laws of Chemistry and Physics.

All living organisms are built up of a substance known as **protoplasm.** This may be termed " living matter," or, in the words of the great zoologist, T. H. Huxley (1825-95), " The physical basis of life." One of the most striking features of living organisms is that their protoplasm is never stable, but is constantly undergoing change. All changes in matter imply the performance of work, which in turn can only be carried out by the use of energy. Every activity, therefore, on the part of a living organism demands the expenditure of energy, and it is for the purpose of obtaining this energy that many of the vital functions are performed.

Though some of this energy is dissipated, usually as heat, much is utilized in the manufacture of fresh material to take the place of that which has been broken down. The sum total of this breaking down and building up again is spoken of as **metabolism.** This cycle is not perpetual, however, since there is an inevitable wastage of energy which must be made good from without. Thus every organism requires an external source of energy to keep its metabolism going.

In adult life these two processes are fairly equally balanced. If building-up is in excess of breaking-down, as in young organisms, there is a definite increase in the amount of protoplasm, resulting in **growth.** On the other hand, if the reverse should occur, as is common in old age, there is a gradual increase of destruction over repair, which will finally result in death, though for various other reasons death may occur even when large quantities of food reserves are present.

Growth, of course, may be observed in non-living matter. A familiar example is the growth of crystals in the chemical laboratory. But this kind of growth is by **accretion,** in which layers of new molecules of the same kind are superimposed upon the existing ones. It differs fundamentally from the type of growth found in organisms, where the fresh molecules, not necessarily of the same kind, are interspersed among those already present, and transformed in such a way that they can be built into the substance of the organism throughout its body. This type of growth is characteristic of living organisms, and is known as **intussusception.**

Break-down is essentially a process of oxidation, as a result of which oxygen is used up and carbon dioxide is formed. This gaseous interchange, with the liberation of energy, constitutes the essential feature of **respiration.** All living organisms, whether animals or plants, continuously respire throughout life. The chief sources of energy are carbohydrates, such as sugars, which are found in the protoplasm and are easily broken down by respiration.

Occasionally substances are formed in the course of metabolism which are put to some special use outside the usual metabolic cycle. These substances are termed **secretions.**

All living organisms exhibit **irritability,** that is they respond to external influences which disturb the metabolic balance. This response generally takes the form of **movement.** The phenomenon of movement varies greatly in degree, and though very marked in animals is not so readily observed in plants owing to their slower reaction to stimuli.

The power of **reproduction** is common to all living organisms, that is to say, the formation of new individuals which are similar to those already existing. In its simplest form reproduction is merely an outcome of the power of growth, involving the separation of part of the body. In this way the race of organisms is perpetuated.

We shall see that all plants exhibit phenomena which are characteristic of life, but that the ways in which these are manifested are often very different.

The protoplasm of even the simplest organism is divided into different parts, a phenomenon spoken of as **differentiation** ; hand in hand with this goes the allotting of special duties to the several parts so differentiated ; this is called **division of physiological labour.** Probably there is no organism without any differentiation at all and with a body consisting of a homogeneous mass of protoplasm, though we shall have occasion to describe some in which there is apparently very little. At the other end of the scale there are organisms, all the parts of whose bodies are differentiated for various functions.

It is this progress towards specialization which forms the basic principle of modern Biology. We can conceive that life first originated in the far-distant past, by some means unknown, as a minute undifferentiated mass of protoplasm. From this start there has been a gradual increase in complexity in the descendants, resulting in highly specialized organisms. This idea of the transition from the less specialized to the more specialized is called **evolution.** The whole world has been populated by evolution with animals and plants which are specialized for their particular surroundings—that is to say, they are **adapted to their environment.**

Differences between Plants and Animals

At the outset of evolution two main lines diverged, resulting in the two great groups of the living world : the **Plant Kingdom** and the **Animal Kingdom.** Different methods of nutrition caused these kingdoms to evolve along completely separate paths, resulting in such radically contrasting types as a tree and the monkey which climbs in it.

Since animals require proteins, and since plants alone have the power of forming them from inorganic substances, it necessarily follows that all animals are dependent upon plants for their food supply.

The other important difference between animals and plants is the result of their different modes of nutrition. Plants are able to obtain the necessaries of life from the air and the soil, which they can find almost anywhere, and as a consequence they have no need of locomotion.

Animals, on the other hand, in their search for ready-made proteins, must move about in order to find their food. Hence, as a general rule, we find that animals have the characteristics of irritability and movement developed to a high degree, whereas plants are stationary and show only slight or sluggish movements in response to stimuli. There are certain exceptions to this general rule. Microscopic plants are often as highly mobile as microscopic animals, while, on the other hand, some animals, such as sponges, are sedentary like plants.

The plant-like type of nutrition is called **holophytic** and the animal-like type is called **holozoic.**

The holophytic mode of nutrition produces large quantities of the carbohydrate substance **cellulose.** This contributes largely to the rigidity of the plant framework, which is not inconsistent with a stationary mode of life, though it would be a serious hindrance to an animal. Cellulose is not formed by any animal and is therefore a distinctive mark of vegetable nature.

Primitive animals are very much like primitive plants : indeed, there are some organisms which can be put into either category, since they are able to feed either holozoically or holophytically. For example, *Euglena* is a minute, motile organism, which, under suitable conditions, is able to build up its protein from simple substances in the water around it, like a plant ; but should conditions be unfavourable, it can live as an animal, using protein for its food.

The Plant Kingdom

Having thus indicated the chief distinctions between plants and animals, we must now turn our attention to the different kinds of organisms which belong to the plant kingdom.

For convenience, plants are classified into **phyla,** of which the following are the most important :—

1. **Thallophyta** (Algae, Fungi and Bacteria).
2. **Charophyta** (Stoneworts).
3. **Bryophyta** (Mosses and Liverworts).
4. **Pteridophyta** (Ferns and Horsetails).
5. **Spermatophyta** (Conifers and Flowering Plants).

The first four phyla are collectively called **Cryptogams,** because their reproductive organs were for long unknown, as opposed to the **Spermatophyta** or **Phanerogams,** in which they are easily recognizable in the cones or flowers. Each of these great groups is further subdivided into Orders and Families (see Chapter III).

Perhaps the earliest plants, like the earliest animals, lived in water at a time when the dry land was uninhabited. The evolutionary tendency of plants has been, firstly, to migrate from water to land ; and secondly, to make the modifications necessitated by the change from an aquatic to a terrestrial habitat. The Algae, which include the seaweeds, are forms which live almost exclusively in water ; hence there is little necessity to develop a complex body, since food substances can be obtained directly from the water in which they live. The simpler members consist of a single cell, but in more advanced forms the cells are joined together in groups or in filaments in which every cell retains its individuality and is identical with every other cell. It is only among the more specialized Algae that we find a division of labour and a marked morphological differentiation of the cells, but even then there is nothing approaching the development of the stem, root and leaf of the flowering plant. So long as plants remain supported on all sides by water, their bodies need little or no reinforcing to keep them erect, but in even the simplest land plants some kind of supporting tissue is found to be present. This usually takes the form of hard material, called wood or xylem. In the Bryophyta, which though terrestrial are small plants, *e.g.*, Mosses, supporting tissue is poorly developed and does not consist of wood.

In the Pteridophyta, particularly in the Filicales or Ferns, very large leaves may be developed in association with which a particularly complex woody tissue has arisen.

The Phanerogams have developed both the tree and herbaceous types, but the wood system is more complex than in the ferns. At the present day the herbaceous plant is probably the most successful type of vegetation.

This, then, very briefly is the conception of the range of organisms which are included under the term plants. Many are very different indeed from the wayside herb, or the garden flower with which we are familiar, but they all agree in having one common feature, namely, that they live holophytically.

The essential feature of holophytic nutrition is that food is absorbed entirely in solution, never in solid form. Where the food solution contains organic substances derived from the decay of other organisms the plant is called a **saprophyte.** Where the food is derived from the living body of another organism the plant is called a **parasite.** Such plants are only a minority. Green plants, on the other hand, take up only inorganic substances from which they build up their own organic material. They are said to be **autotrophic,** which means " self-feeding." This mode of nutrition is shown by no organisms except plants, and we may briefly refer to the process here.

First of all the green plant combines the free carbon dioxide of the air with water from the soil, to form carbohydrates. Every green plant obtains its carbohydrates by means of this process of feeding, which is called **carbon assimilation** or **photosynthesis.** This process can take place only in the presence of light and **chlorophyll.**

Chlorophyll is a green pigment of a complex nature, containing carbon, oxygen, hydrogen, nitrogen and magnesium. It is found in all the green parts of plants, particularly in the leaves, where it occurs in specialized protoplasmic structures which are known as **chloroplasts.** Only in cells containing chloroplasts can the photosynthetic production of carbohydrates take place. The necessary water and some mineral salts in solution are either obtained directly from the water in which the plants live or, in land plants, from the soil through the **roots.** In the body of the plant certain of these salts containing nitrogen are combined with carbohydrates to form proteins and, finally, protoplasm.

CHAPTER II

CYTOLOGY

THE term Cytology denotes the study of the internal structure of the cell, as distinct from Histology or the structure of tissues. The limit of Cytology proper is, therefore, set by the cell wall, but within that boundary we have to deal with the living substance, protoplasm itself, a material of paramount importance but of so complex a nature that the use of every means of investigation, physical, chemical and microscopical, has not yet succeeded in penetrating all its secrets.

In this Chapter we shall deal chiefly with observations on the microscopical level, that is to say with visible structures, but we shall return later, in Volume IV., to some deeper considerations of the ultimate structure of protoplasm on the molecular level, for the understanding of which some knowledge of colloids is necessary.

The word " cell " was first used by Robert Hooke in 1665 in his " Micrographia," where he compares the structure of cork to that of a honeycomb. He, of course, saw only the cell walls, so that the primary meaning of the word was that of a space enclosed by a wall.*

The fundamental feature about a cell is that it is both a structural and a functional unity. Within a material boundary surface there is a portion of protoplasm which is visibly separate and distinct from other portions, and is organised as a self-sustaining and self-propagating physiological system. A cell which is a part of a higher organism is not wholly independent. Its activities are co-ordinated with those of other cells in the life of the organism of which it is a part. Such cells may, however, possess the ability to live independently for varying periods, when separated, and it is fallacious to draw a sharp distinction between them and cells which live a permanently independent life, or to deny that " unicellular " organisms are in fact cells as well as organisms. From the most general point of view the unitary organization is the essential feature of a cell and the details of its internal structure, *i.e.*, whether it possesses or lacks any of the features commonly found in cells, are matters of indifference.

A higher organism should not be thought of as an aggregate or colony of individual cell-organisms. During development the cells of such an organism arise through the progressive subdivision of its substance. They are localised centres of functional activity, and the organism gains in efficiency from this distribution of its activities. The status and the capacity

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* The cells of animal tissues are usually surrounded by relatively delicate membranes, sometimes referred to as " intercellular substance." This is usually composed of nitrogenous material, either a form of protein, such as collagen or related substances such as chitin. Cellulose only occurs very rarely. Whether these walls are simply modified protoplasmic surfaces or are metabolic substances formed by the protoplasm, as in plants, is not certain.

for independence of each cell depend on the extent of the functions which devolve upon it in the process of subdivision, but so long as it remains a part of the structure of the higher organism, it remains also functionally integrated into the life of the whole.

In the simplest multicellular organisms all the cells are seemingly equivalent and all are potentially independent, but they are nevertheless integrated parts of a whole, and this is seen from the fact that even in these simple cases potential differences may exist which are only revealed at certain times or under certain circumstances. Every advance from this level has been associated with increasing differentiation between cells, at first purely functional, but later structural as well, leading at length to such high degrees of specialization that even the bodies of dead cells may be of essential service to the organism. Differentiation is not something added to organization, it is a necessity of organization, and differentiation of cells is inherent in the nature of the multicellular condition even at its simplest.

The essential material in every living cell is the **protoplasm**, the wall being no more than a protective covering secreted by it, but protoplasm was not recognized as the living substance until 1835, when it was named " sarcode " by Dujardin. Its universal importance was announced by Ferdinand Cohn in 1850, and the name protoplasm, used a few years before by von Mohl, gradually replaced the earlier term. Curiously enough the discovery of the cell nucleus by Robert Brown in 1831 came before that of protoplasm. Although the nucleus is itself protoplasmic, it is usually denser and is more easily seen than other parts of the living matter.

That cells are individual entities, the bricks out of which all living bodies are built, was the view advanced by Schleiden and Schwann, about the year 1838, under the title of the Cell Theory. Its truth has long been firmly established, and every investigation has only strengthened our belief in the fundamental character of the cell as the unit of living organization in all higher plants and animals. Whether unicellular organisms are equivalent to single cells of a tissue, or to complete organisms, is a moot point. All we can say definitely is that the organization of protoplasm into self-centred units is co-extensive with life itself. In fact we know nothing of life as such, we only know living organisms.

The essential structures comprised in a plant cell (Fig. 1) may be summarized as follows :—

1. The **Cell Wall,** basically composed of cellulose but often chemically altered by the incorporation of other materials. This encloses a space, the **Cell Lumen,** in which the following occur.

2. The **Cytoplasm,** which includes all the protoplasm outside the nucleus, with certain differentiated structures :—

The **Plasma Membrane,** an external surface layer in contact with the wall.

The **Vacuolar Membrane** or **Tonoplast,** bounding the vacuoles.

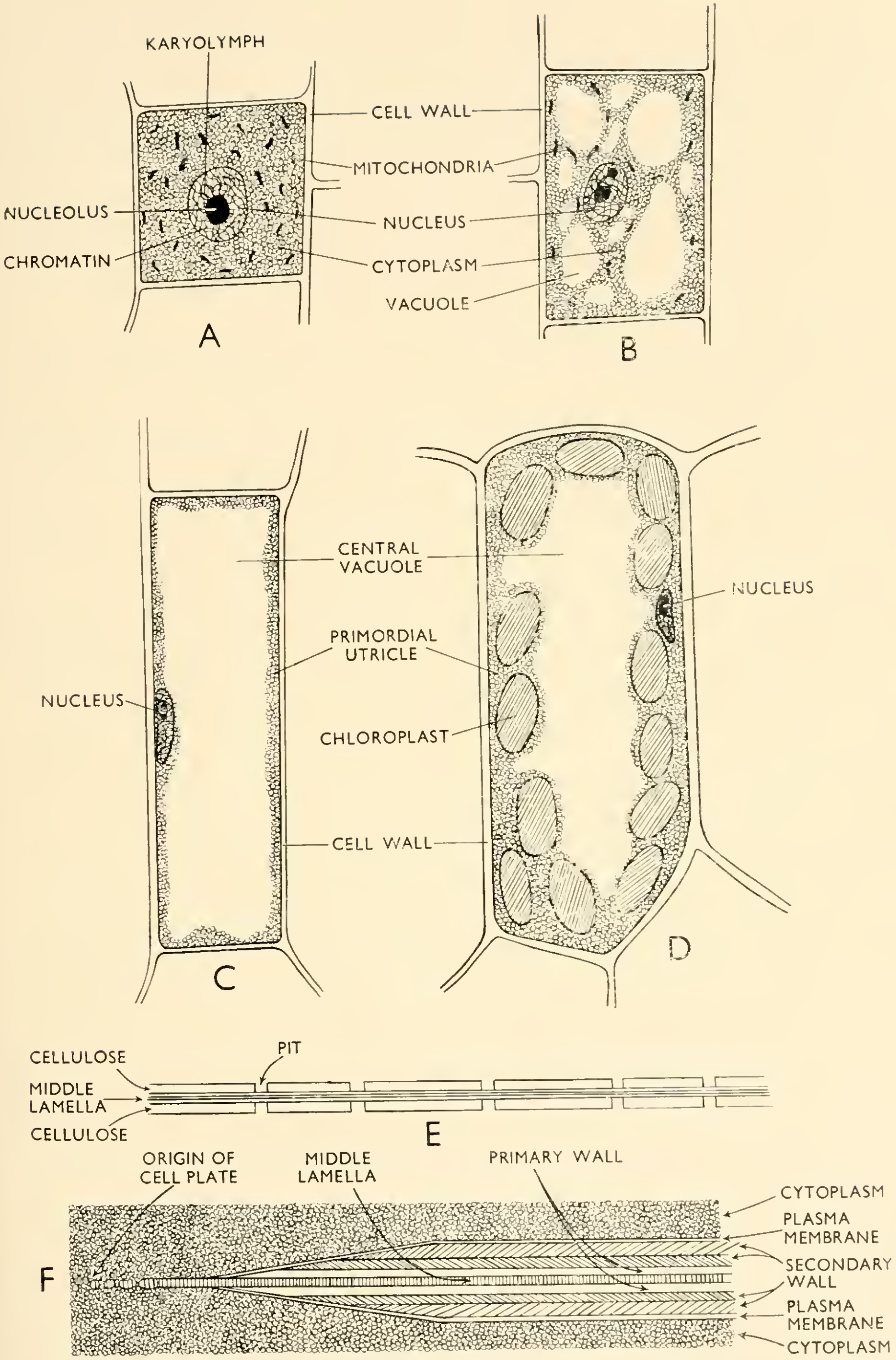


Fig. 1.—Diagrams to illustrate the structural features of simple plant cells. A, In the young condition, as found near the growing points. No vacuoles are present. B, Somewhat older state with vacuoles developing. C, Mature state, with a single central vacuole and the cytoplasm confined to the walls. D, Mature cell containing chloroplasts. E, Details of the primary wall structure. F, The development of the various layers of the complete cell wall, from the cell plate formed during cell division. (F *modified from Sharp.*)

Embedded in the cytoplasm are the following structures :—

- (*a*) The **Plastids,** which are protoplasmic bodies, denser than the cytoplasm and not separated from it by any definite membrane. They comprise :—
    - Chloroplasts, the bearers of the green pigment, Chlorophyll.
    - Chromoplasts, with colours other than green (the term is sometimes used to include all coloured plastids).
    - Leucoplasts, which are colourless and found chiefly in underground organs and in the meristem cells.
- (*b*) The **Vacuoles,** sac-like enclosures in the cytoplasm, filled with a liquid " cell-sap."
- (*c*) The **Mitochondria** or Chondriosomes, granules, rods or threads apparently composed of phospholipins and proteins, which are found scattered through the cytoplasm of all cells.
- (*d*) The **Centrosomes,** granules associated with nuclear division, which are characteristic of animals, but are found only in a few of the lower plants.
- (*e*) The **Ergastic Substances,** or materials secreted by the cytoplasm either as food materials or as by-products. Here are included such things as oil-drops, protein grains or crystalloids, starch grains (in the plastids) and crystals of Calcium oxalate.

3. The **Nucleus,** almost always single in the cell and composed of the following parts :—

- (*a*) The **Nuclear Membrane,** separating it from the cytoplasm.
- (*b*) The **Chromatin,** which is organised as :—
    - The Nuclear Reticulum, formed of fine threads, which is characteristic of the non-dividing or " metabolic " nucleus.
    - The Chromosomes, which are relatively thick rods, formed from the nuclear reticulum during nuclear division and constant both in number and form. Chromatin is a compound of nucleic acid with basic protein.
- (*c*) The **Nuclear Sap,** or Karyolymph, which is colourless and fills all the central parts of the nucleus. It may also contain ergastic reserves, *e.g.*, protein crystals.
- (*d*) The **Nucleolus,** one or more in each nucleus, which is a spherical granule of material, attached to the reticulum and associated with certain chromosomes. It consists of a mixture of protein and lipin, and normally stains differently from the chromatin.

A cell in a higher organism cannot be looked upon as an independent unit. There is a considerable degree of physiological unity pervading all tissues and the cell must be largely controlled by the functioning of the tissues as a whole. Although itself a synthesis of many smaller components, as we have seen above, it plays a part in the synthesis of a still higher unit, the organism, to which it is subordinate. Modern studies no longer treat the cell as a static object but as a functioning mechanism, and the growth of experimental cytology, including the micro-dissection of cells, has opened roads of the highest promise towards a fuller understanding of life processes.

We will now consider the more important cell components in order.

THE CELL WALL

The primary wall is laid down at **cytokinesis** or cell-division. In many lower plants, and in the formation of spores in many plants of all grades, the cytoplasm divides by furrowing, that is by the formation of a cleavage plane which develops inwards from the old wall towards the centre of the cell. In the great majority of cell divisions, on the other hand, the two daughter cells are separated by a **cell plate,** which forms between the two daughter nuclei towards the end of the nuclear division process. The cell plate first appears near the middle of the cell and grows outwards until its edges touch the old wall and join it.

The cell plate is at first a fluid film, but it is soon solidified by the deposition in it of pectin and protein. The latter soon disappears from new cell walls in mature tissues, but it seems to be more persistent in the cell walls of meristematic tissues. This first solid layer forms the intercellular matrix or **middle lamella.** Its subsequent changes of composition are not yet clear, but it seems probable that the pectin or pectinic acids first present become combined with cellulose to produce an insoluble substance closely resembling pectose, and that Calcium later enters into its composition, perhaps in the form of Calcium pectate. In woody tissues, however, the middle lamella may become intensely lignified (about 70 per cent.) and pectic substances disappear or are at least masked.

While the middle lamella is still quite young a thin cellulose layer is deposited on each side of it, and the three layers together constitute the **primary wall.** No further development of this wall takes place until the cell ceases to divide, except that the new middle lamella grows into the surrounding walls and becomes continuous with their middle lamellae.

When a cell has ceased to grow and divide it may develop a **secondary wall.** This also consists of three layers, of which the middle one is much the thickest. All three contain cellulose, but the thin outer and inner layers contain more pectic substances than the middle layer. When lignification of the wall occurs the lignin substances are laid down chiefly in the thick cellulose layer, in the form of longitudinal radial plates, rich in lignin, divided by layers rich in cellulose. Even in the walls of a woody cell there is thus a large amount of cellulose, with which the lignin is mixed or perhaps chemically combined.

The deposition of the secondary wall layers is seldom, if ever, perfectly uniform ; there are commonly a number of unthickened spots, which are called **pits,** at which the cells are separated only by the primary wall. Through this thin partition there frequently run extremely fine protoplasmic threads, the **plasmodesma** or intercellular connections. Although the plasmodesma are characteristic of the pit areas they are not necessarily confined to them, and in some cells with very thick secondary walls, for example in the storage tissues of some seeds, they may be seen to penetrate the whole thickness of the wall.

How these plasmodesma are formed is still uncertain. Formerly it was supposed that they were the remains of protoplasmic fibrils which connect the two daughter nuclei after a division. If this were true they could only occur between sister cells, which is certainly not the case. On the other hand, it is difficult to believe that such fine threads could bore their way through a wall already formed. It would therefore seem probable that they are established at an early stage, when the cells are separated only by the soft matrix or middle lamella. The presence of protein in the young lamella probably indicates that it is permeated by the cytoplasm. At this stage they may be very numerous, but they occur in groups, and although some may be obliterated as the cell matures, these groups are, in general, the sites at which pits are formed. That the plasmodesma actually provide protoplasmic continuity from cell to cell is shown by the fact that infecting viruses (p. 361) will only pass through cell walls where plasmodesma are present.

The cellulose wall is doubly refractive, and it may therefore be concluded that it is crystalline in structure. The nature of the molecular arrangement is not, however, indisputably settled. The most generally held view is that which originated in the researches of Nägeli in 1863, who called the crystalline units of the cell wall structure **micellae.** Analysis of cellulose with X-rays by Preston and others shows a fibrillar structure, due to the linking together of β-glucose molecules into chains about 500 Angström units long by about 50 Angström units thick. As the single glucose molecule measures about 5 Angström units in length, a chain of 1,000 would be about 5,000 Angström units or $0 \cdot 5\mu$ long, which is within the microscopic range. Adjacent chains lie parallel to one another and about 100 of them constitute one micelle. The latter in turn are aggregated into " fibrils," which give rise to the striations visible in the wall, especially after treatment with a swelling agent, the striations being probably slip-planes due to mechanical displacement of the fibrils. In addition to cellulose there seems to be some pectic material and some wax present, mixed with the cellulose and probably forming a matrix around the cellulose units. The orientation of the fibrils is spirally around the cell at varying degrees of inclination to the long axis, the thickness of the wall being apparently built up of a series of successive sheets of micelles or of fibre units, the inclination of the spiral being different in successive sheets and changing as the proportions of the cell change during growth. The angle of the spiral is more nearly longitudinal in the thick layer of the wall and more nearly transverse in the thin layers, though it is very variable. The molecular pattern exposed at the inner surface, where it is in contact with the cytoplasm, apparently acts as a molecular mould for the building in of fresh glucose units into the cellulose pattern.

The growth of the cell in length does not involve any stretching of the existing cellulose chains, for the forces holding their glucose units together are much too great for this to be possible. It is due either to the intercalation of new sets of fibrils between those already existing or to their growth in length by the addition of new glucose molecules. Growth by this intercalation process is called **intussusception** and is characteristic of the young phase of the cell, while the addition of successive thickening layers, concentrically, is called **apposition** and is a feature of cell maturity.

Secondary cell walls often show a visible structure of concentric layers. These are not, of course, single sheets of cellulose molecules, but seem to represent variations in the amount of cellulosic and non-cellulosic material present. In the wall of the cotton fibre it has been possible to correlate these concentric layers with the daily metabolic cycle, the denser layers representing deposition by day, and the lighter layers being formed during the night. They are analogous to the growth rings in trees, and are similarly affected by variations in the environment at different times. They can be definitely dated, and the corresponding layers in the cell walls in neighbouring plants are found to be similar.

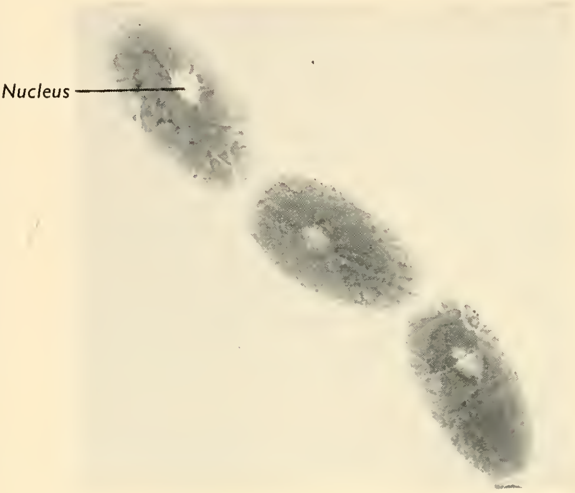


Fig. 2.—*Tradescantia virginiana.* Cells of a staminal hair, showing nuclei and strands of cytoplasm in which streaming movements take place. The vacuole contains a solution of a purple pigment.

CYTOPLASM

The living cytoplasm, where it can be observed in uninjured cells, appears as a colourless, viscous fluid, which frequently shows streaming movements or a circulation round the cell, called **cyclosis** (Fig. 2). This striking movement of the living substance has been the subject of a great deal of investigation but no final explanation has emerged. The energy is certainly provided by respiration, and the most probable view of the mechanism is that it is due to rhythmic contraction and relaxation of the protoplasmic structure.

Cytoplasm is not homogeneous in appearance. There is a hyaline fluid medium, which shows no microscopic structure, called the **hyaloplasm,** in which are suspended immense numbers of minute granules or droplets consisting of ergastic substances, including oil-drops, protein, volutin and lipin granules, and the larger more definitely visible granules known as **mitochondria.** None of these is an essential component of the cytoplasm itself, which is the hyaloplasm, and they can be centrifuged out of suspension in the hyaloplasm without injuring it. It is in the hyaloplasm, therefore, that the true living structure of protoplasm must be looked for.

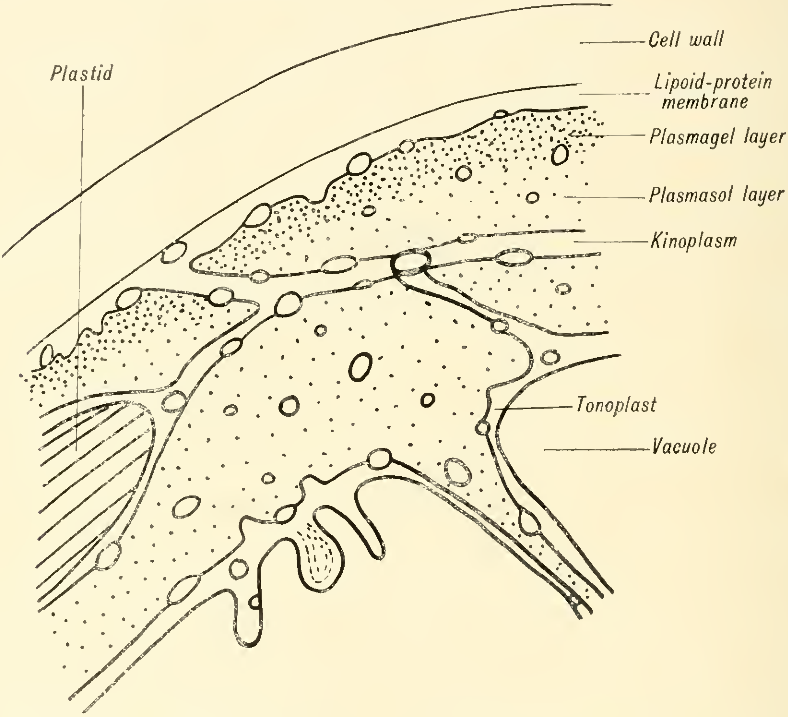


Fig. 3.—Diagram of the structure of the cytoplasmic utricle in a typical cell, very highly magnified. (*After Seifriz.*)

The cytoplasm is usually differentiated into zones (Fig. 3). Firstly, there is a very thin external layer of hyaloplasm with relatively few granules, which has sometimes been called the **ectoplasm,** but is more properly described as the **hyaline layer,** as the term ectoplasm has been differently employed in *Amoeba.* In plant cells this hyaline layer is fluid and extremely thin. It is most easily revealed in the form of the very fine extensions which often connect a plasmolyzed protoplast to the pit areas of the cell wall. Thin as it is, it possesses a coherent surface film, probably a monomolecular layer of non-aqueous substance, which is referred to as the **protoplasmic membrane**, or sometimes the **plasmalemma.** A similar but tougher membrane forms the boundaries of the vacuoles and is called the **tonoplast.**

The portion of the cytoplasm which is enclosed by these two layers shows the granular appearance previously mentioned, and is known as the **endoplasm.** This part of the cytoplasm is differentiated into three component systems. The outer portion (the ectoplasm of *Amoeba*) next to the hyaline layer, is elastic and almost solid (geloid) in texture, while the inner portion is definitely fluid and much less cohesive than the outer layer.

When protoplasm is immersed in water the external layer remains coherent, but if this is ruptured the internal portion mixes readily with the water. The external membrane appears to consist of a mixture of lipin and protein molecules, and is probably of molecular thickness, but it is the controlling agent in determining the entry of substances into the cell or, as it is called, the **protoplasmic permeability.** For example, the dye, Eosine, will not enter a living cell, but if it is injected through the protoplasmic membrane it diffuses readily in the liquid endoplasm.

A third component, called **kinoplasm,** has been distinguished, consisting of a system of very delicate fibrils, only visible with difficulty, but distinguishable by the streams of granules which they carry along. The kinoplasm appears to be connected to both the inner and outer protoplasmic membranes.

It would be a mistake to view these protoplasmic systems as fixed and permanent structures. The most essential characteristic of protoplasm is its changeability, and not only do reversible alterations occur in the different components but probably a continuous exchange of material occurs between them.

The *living* quality of protoplasm lies in the interaction of its components, not in the properties of any individual part of it. It is an active *system*, neither a substance nor simply a mixture of substances, but a chemical machine in which all the components have a part to play which may be more or less essential to the whole.

The **vacuoles** are part of the cytoplasmic system, though in a mature plant cell only one large vacuole may be present, occupying the whole central part of the cell and confining the cytoplasm to a thin peripheral layer, the **protoplasmic utricle.** In the youngest cells, however, either no vacuoles occur or they are very small, and one of the main features of the development of cells towards maturity is the appearance of vacuoles in the cytoplasm, a process called **vacuolization.** It is still an open question if vacuoles arise *de novo* in cells, but the weight of evidence seems to be on the side of the view which regards them as always present, even in meristematic cells. Large vacuoles are probably derived chiefly from the growth and fusion of small pre-existing ones. Passing through a phase which suggests a network of canals, possibly due to cytoplasmic streaming movements, these separate vacuoles eventually fuse into larger units or even finally into one. The **cell sap,** which the vacuoles contain, is an assemblage of practically all the materials which figure in metabolism, from inorganic salts to enzymes and even proteins. Some of these, notably the sugars and organic acids, are highly osmotic, and are the cause of the **osmosis** by which water is drawn in through the cytoplasm. The entry of water creates a positive pressure in the vacuole, which is called the **turgor pressure,** by means of which the cell as a whole is kept extended. It is interesting to note that the concentrations of some inorganic salts in the vacuole may be different from that outside, showing that the function of the protoplasm in absorption is by no means merely passive.

The term **mitochondria** is applied to granular elements found in the cytoplasm, some of which are relatively large or filamentous, and readily recognizable even in living cells. Granules of all sizes occur, however, and it is not certain where the limit should be drawn, or whether all particles down to visible limits should be included under this name. There is in cytoplasm a certain class of granules, or short rods with certain chemical properties in common, which may be regarded as true mitochondria. They disintegrate in highly acid or alkaline solutions, and consist of a mixture or compound of phospho-lipins and nucleo-proteins. The nucleic acid involved here is, however, not the same as that in the nucleus itself, as described later, but is ribo-nucleic acid, a cytoplasmic material, which may also occur free in the form of granules, named originally **volutin grains.**

The universal occurrence of mitochondria suggests that they have some metabolic function, but although theories have been plentiful, facts are scarce and no definite statement can yet be made on the subject.

The **plastids** are persistent cell organs, which appear to arise from minute granules present in the youngest cells and ultimately derived from the oosphere. These pro-plastids have often been confused with mitochondria, and whether they are distinct structural elements is still uncertain. The mature **chloroplast** has been the subject of intensive research on account of its importance in photosynthesis. The variability of its form in the Algae is as striking as is its constancy of character in all the higher plants. This constant form is roughly that of a disc, like a watch, with convex faces, which seems to have proved so efficient that it has remained unchanged through vast periods of evolution. Fully grown chloroplasts multiply in the cells by a process of division. The plastid elongates and a median constriction or waist appears, which narrows until the two halves are completely separated. The plastid is protoplasmic in nature, though of gel consistency, and there is evidence that it has a semipermeable surface membrane. The protoplasmic body or **stroma** is colourless, but in chloroplasts it includes numerous small bodies, called **grana,** composed of protein and lipoid, which contain the chlorophyll. Where these are large and not too closely packed, as in many Mosses, they may be seen as green spots, giving the plastid a mottled appearance.

In the Algae the chloroplasts may contain a protein body called the **pyrenoid,** around which the starch grains are formed during photosynthesis.

Leucoplasts are similar in development and structure but lack chlorophyll. Some at least, however, form chlorophyll when they are exposed to light, as in potato tubers.

Whether the plastids are in fact permanent cell structures cannot yet be decided. In some plants, notably Mosses, they can be traced through the reproductive cells from one generation to the next, but in most cases the idea of permanence rests on supposition, as the pro-plastids cannot be adequately distinguished from other cell granules.

THE NUCLEUS

Every normal cell has one nucleus, and one only. Exceptions to this rule are rare, except in Fungi and in some reproductive structures. The Bacteria and the Cyanophyceae have no nucleus as it is understood in higher plants, though their cells may contain nuclear substances. In some Thallophyta large cells occur containing many small nuclei, and these structures are called **coenocytes** on the supposition that they may be really compound cells.

The fully developed nucleus, like the chloroplast, is an organ of remarkable uniformity, not only over great groups of the plant kingdom but throughout most of the animal world as well. This means that the structure of the nucleus is fundamental to the organization of the living cell, and that conclusions drawn from its study must have a close bearing on the general problems of vitality. The nucleus is in many ways the centre of the life of the cell. If a cell is deprived of its nucleus it may continue to respire for some time, but it does not grow or reproduce. Whether the nucleus or the cytoplasm is the more ancient, that is to say which came first in evolution, cannot be definitely answered, but as some lowly organisms have no nuclei it seems possible that the nucleus was secondary, at least in its fully organized form.

Nucleus and cytoplasm are separated by the **nuclear membrane** (Fig. 4), which seems to be a cytoplasmic structure like the tonoplast, but more delicate and less permanent. The nucleus it surrounds is usually more or

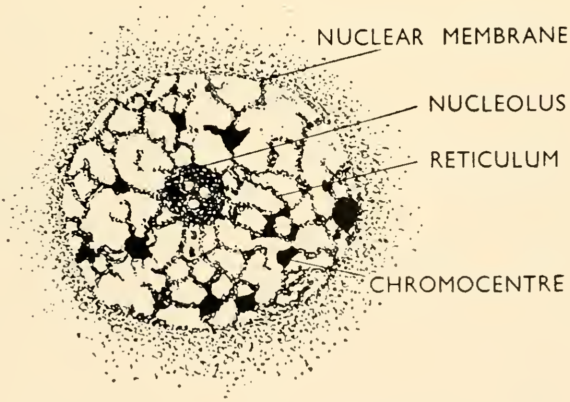
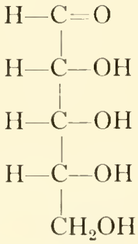


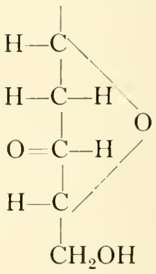
FIG. 4.—*Vicia faba.* Diagram of the structure of a nucleus in the " metabolic " or " resting " condition. (*After Fraser and Snell.*)

less spherical. Inside the membrane is the **karyolymph** or nuclear sap, resembling the cell sap, except that it is very viscous and sometimes almost solid. In some respects therefore the nucleus may be looked upon as a special kind of vacuole. Where it differs from other vacuoles is in containing the substance **chromatin,** which plays an entirely special role in the cell. In it are located those factors which control the development of the cell and hence the development of the whole organism, and serve, moreover, to transmit the same characteristics to the following generation. In short, the chromatin is the seat of the mechanism of heredity which maintains the continuity of the species.

The chromatin is visible as a spherical network of fine threads inside the nuclear membrane and in contact with it. This is called the **reticulum** of the nucleus, and it consists of simple proteins of the protamine and histone types. These are basic substances and they therefore stain easily with acid dyes. The nuclear surface is probably the seat of protein synthesis in the cell so that these proteins are formed *in situ.* At many points of the reticulum are seen lumps or knots of material which stain differently, chiefly with basic dyes. This is due to the fact that they contain thymo-nucleic acid, and they are spoken of as **heterochromatin,** while the rest of the reticulum is called **euchromatin.**



d-ribose $C_5H_{10}O_5$.



desoxy-ribose $C_5H_8O_3$.

Thymo-nucleic acid differs from the ribo-nucleic acid that we spoke of in connection with mitochondria. The chief difference lies in the sugar which forms part of the molecule. In ribo-nucleic acid there is, as the name implies, ribose, a stable sugar which can be isolated as a pure substance. In thymo-nucleic acid, on the other hand, ribose is replaced by a molecular group, desoxy-ribose, which only exists in combination with other molecules, and which has a strong tendency towards the linking of its molecules to one another in long chains to produce complexes or " polymers " of as many as 6000 molecules, arranged in a similar manner to the molecules in the protamine proteins. This substance can be identified microscopically by a staining reaction known as the Feulgen Test,* and its presence is taken as indicative of the existence of chromatin in a cell.

In addition to the reticulum each nucleus contains one or two rounded bodies called **nucleoli,** which are attached to part of the reticulum. The nucleolus

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* Thymo-nucleic acid, set free by hydrolysis of chromatin, gives a purple colour when treated with Basic magenta decolorized by Sodium sulphite.

is not formed of chromatin. It consists of histone protein, with phospholipins and ribo-nucleic acid, that is to say, it has chemical affinities with the mitochondria. It is always attached to one part of the chromatin reticulum, and there seems to be an active exchange of material between the two.

The nucleus in this condition is properly called the **metabolic nucleus,** for its chief activity is in connection with cell metabolism. To distinguish it from the nucleus in active division it is sometimes also described as the resting nucleus or the interphase nucleus, though the latter term only applies properly to tissues in which nuclear division is still active.

Mitosis or Nuclear Division

Nuclear division precedes cell division. The frequency with which cell division takes place depends on many factors and naturally is greatest in young cells in a condition of active growth, although even old, differentiated tissue-cells may divide occasionally. In many plants a daily rhythm can be traced, divisions in root tips being most active at about midday and in stem apices about midnight.

The process of nuclear division is called **mitosis** (Gr. *mitos*, a thread) with reference to the fibrils of cytoplasm which play an important part in it. An older name, **karyokinesis,** is now rarely used.

There is another form of nuclear division called **amitosis,** in which no fibrils appear and the nucleus divides directly into two, by constriction, without change of structure. Amitosis in plants is only found in certain specialized tissues. It is still uncertain whether it is ever accompanied by cell-division, and the balance of evidence is against it being a phenomenon of cellular reproduction.

Mitosis takes place in a regular series of four phases, of which the first is the **prophase** (Fig. 5). This first stage involves the resolution of the

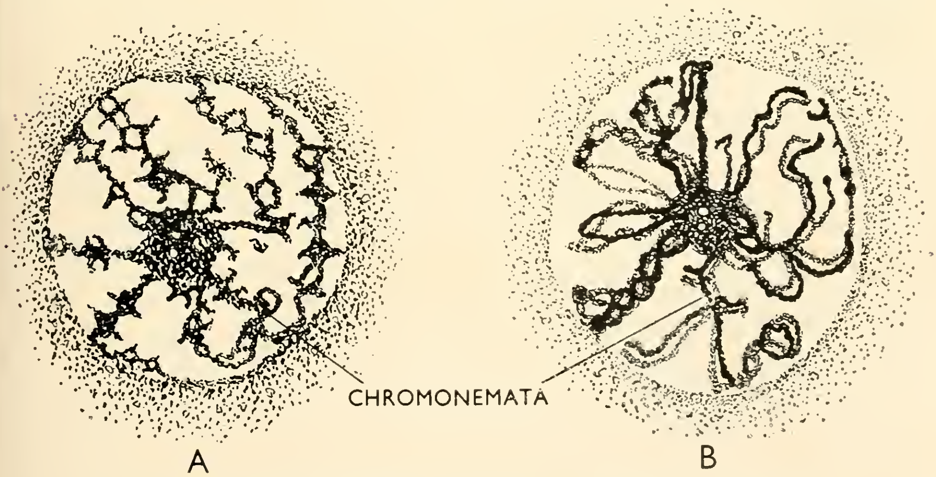

Fig. 5.—*Vicia faba.* Diagrams of two successive stages, A and B, in the prophase of mitosis. (*After Fraser and Snell.*)

chromatin reticulum in the metabolic nucleus into a number of thin, separate threads, the **chromonemata,** which do not stain very deeply. Each of these chromonemata is double. The two together represent one **chromosome,** and each individual thread or half-chromosome is also called a **chromatid,** for convenience in tracing it through the subsequent changes.

Each chromatid shows a double series of spiral coilings or **gyres.** Firstly, the two members of a pair are loosely twisted round each other (relational coiling), these coils being **relic coils,** left over from the previous mitosis. As prophase advances the relic coils disappear and a new series of minor gyres develops, each chromatid coiling independently.

The two chromonemata of each pair are linked together at one point, where there is an unstained spot or granule, known as the **kinetochore** or **centromere,** usually situated not far from one end. Its function will appear later. The portions of the chromosome on each side of the kinetochore are called the **arms.**

As prophase draws to a close three things happen. Firstly, the chromonemata begin to uncoil, so that the gyres are fewer and larger. Secondly, a densely stainable **matrix** begins to accrete around each chromatid, forming a double, thickened chromosome (Fig. 6). Thirdly, each chromonema splits lengthways, so that each chromatid now contains, within the matrix, two chromonemata which are relationally twisted together as well as coiled. The entire chromosome at this stage therefore consists of two thickened chromatids, conjoined at the kinetochore, and in each chromatid there are two chromonemata. The chromosomes shorten and become thicker and denser, and the coils of the chromonemata become closer. In this condition they enter the **metaphase** (Fig. 7).

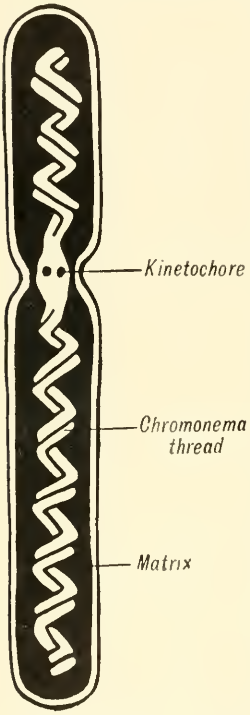

FIG. 6.—Diagram of the structure of a half metaphasic chromosome, *i.e.*, a chromatid. (*After Schrader.*)

The nuclear membrane now disappears, so that the chromosomes are no longer separated from the cytoplasm, and the nucleolus also disappears. The chromosomes arrange themselves across the middle plane of the cell, forming the **equatorial plate.** If the chromosomes are short they may lie horizontally on the plate, but if they are long it may be only the portions containing the kinetochore which actually lie on the plate, the arms pointing in different directions.

The kinetochores then divide, so that the chromatids separate and become independent chromosomes. Simultaneously two sets of fine kinoplasmic fibrils appear, one on each side of the nucleus, converging towards the two opposite poles of the cell. These are the **spindle fibres,** and together they make up a double-ended cone, the **achromatic spindle,** so called because of its slight affinity for stains. Studies by micro-dissection have shown that the spindle is not a mere appearance in the cytoplasm, but a definite body,

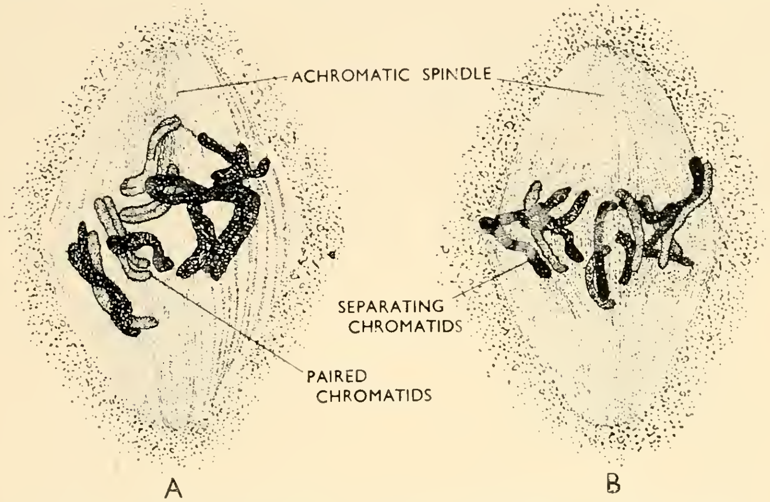

FIG. 7.—*Vicia faba*. Diagrams of two successive stages, A and B, in the metaphase of mitosis. (*After Fraser and Snell.*)

which can be extracted entire from the cell, with the enclosed chromosomes. One end of each spindle fibre is attached to the kinetochore of a chromosome. There is indeed some evidence that the kinetochores may be concerned in their formation by the secretion of nuclear material. At any rate if a chromosome loses its kinetochore it has no spindle attachment and can take no part in the subsequent movements.

The next stage, or **anaphase** (Fig. 8) opens with the chromosomes

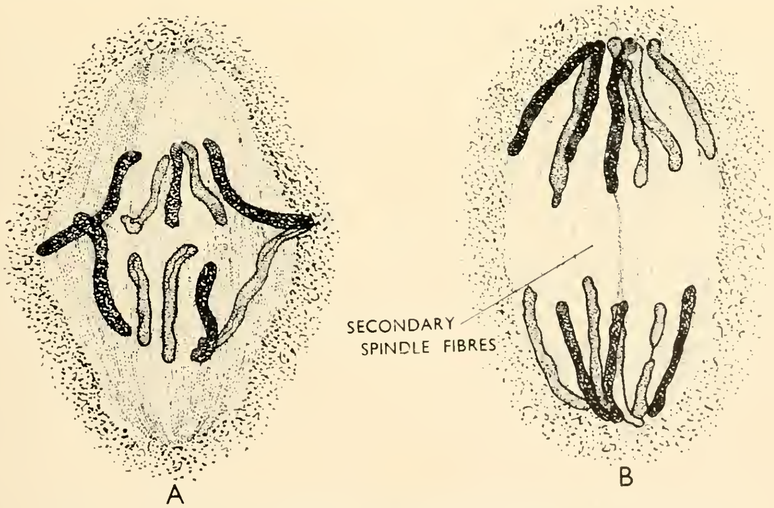

FIG. 8.—*Vicia faba*. Diagram of two successive stages, A and B, in the anaphase of mitosis. (*After Fraser and Snell.*)

moving away from the equatorial plate in two groups, one of the two chromatids of each original chromosome going into each group. The distribution of chromosomes into the two groups is thus exactly equal, in a qualitative as well as a quantitative sense, and the division is said to be **equational.** The two groups move convergently towards the two poles of the spindle and form a very characteristic figure, of two radiating clusters, known as a **diaster.** In this movement the kinetochores lead the way, the arms trailing behind, so that the chromosome looks as if folded in two. As the chromosomes approach the poles the matrix gradually disappears and the double chromonemata again come into view. Their coils relax and they lengthen out, though they retain the relational twist round each other until the prophase of the next mitosis.

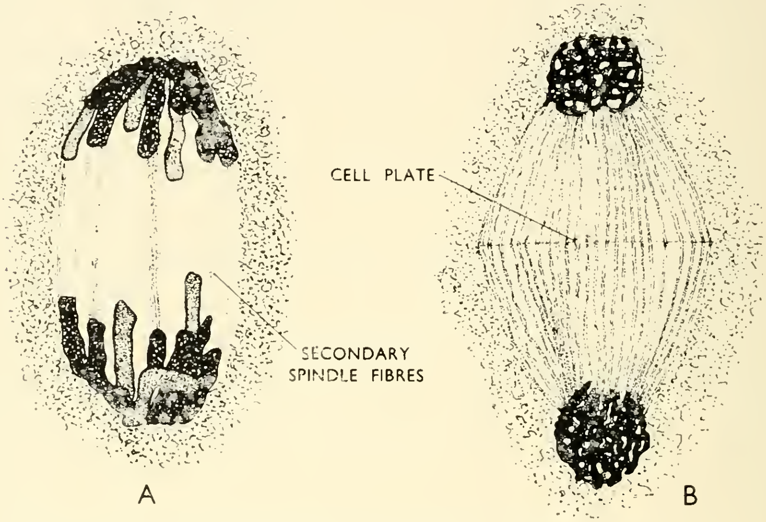

Fig. 9.—*Vicia faba.* Diagram of two successive stages, A and B, in the telophase of mitosis. (*After Fraser and Snell.*)

The cause of the movement is still uncertain and has aroused a good deal of controversy, but it is not unlikely that there is, as was first supposed, a real tractive force exercised by the spindle fibres, due to the contraction of the long protein molecules of which they are composed.

Mitosis now enters the **telophase** (Fig. 9), during which the two daughter nuclei are organized. The chromonemata arrange themselves into a reticulum, and in the process they appear to become linked together. If there is any considerable interval between divisions, a finely granular reticulum is formed, in which the individual chromonemata become indistinguishable, but if divisions follow one another rapidly the reticulum may not be completed and the next prophase follows almost directly.

Nuclear membranes now appear round the daughter nuclei, and the nucleolus is reformed in each. The relation of the latter body to the chromosomes is peculiar and interesting. Among the chromosomes in a diploid nucleus there is always one pair which show a marked constriction near one end, on which no matrix accumulates. The small terminal portion, beyond the constriction, is thus isolated from the main body of the chromosome and is termed a **satellite,** while the chromosomes themselves are known as the **sat-chromosomes.*** This constriction is associated with the formation of the nucleolus and is called the **nucleolar organizer.** The nucleolus makes its appearance attached to the base of this constriction, which is usually heterochromatic (see below), and as the nucleolus enlarges the satellites may adhere to its surface. The nucleolar material is apparently secreted by the sat-chromosomes during telophase, while during prophase it is dissipated. It is either adsorbed on to the chromosomal surface as a pellicle, or, according to another view, it is wholly or in part dispersed into the cytoplasm. As we have already mentioned, it contains ribo-nucleic acid, which is found in cytoplasm, especially in the mitochondria.

There is at least one pair of sat-chromosomes in a diploid nucleus and each of them forms a nucleolus. If they happen to lie close together at telophase the two nucleoli may coalesce into one, otherwise they remain apart. The presence of more than two nucleoli in a nucleus is usually a sign that more than the diploid complement of chromosomes is present, that is to say that the nucleus is **polyploid.**

The matrix of the metaphase chromosomes is known to consist of thymo-nucleic acid, the molecules of which align themselves in rows, parallel to the protamine molecules of the chromonemata. Underlying the other changes during mitosis there is thus a cycle of the charging and discharging of nucleic acid upon the chromonemata. Certain parts of a chromonema may, however, retain their charge throughout the metabolic phase ; these portions remaining deeply stained in telophase and even in the metabolic nucleus, where they may be seen as knots or **chromocentres** in the reticulum. This retained material is called **heterochromatin,** and the rest is distinguished as **euchromatin.** A chromonema which carries heterochromatin is called **heteropycnotic.** Charges of heterochromatin occur most commonly near the kinetochore and near the nucleolar organizer in sat-chromosomes. The heterochromatin appears to be responsible for the formation of the thymo-nucleic acid of the euchromatin in the rest of the matrix and possibly also for the ribo-nucleic acid of the nucleolus, since the latter always appears in contact with a heterochromatic region.

The chromonema itself is not uniform throughout its length, but shows a beaded structure, in which the beads or **chromomeres** stain more deeply than the intervening portions. These chromomeres are the centres of attachment of the matrix substance. They are generally regarded as the seats of the **genes** or units of heredity, which we shall speak about under Genetics.

The chromosomes which are formed in mitosis have always a constant and characteristic number in every true species of plant and animal (see table on p. 33), and they are also constant in form. Each chromosome in a set has a definite length, thickness and shape, so that it can be recognized at

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* " Sat " stands for *Sine Acido Thymonucleinicus.*

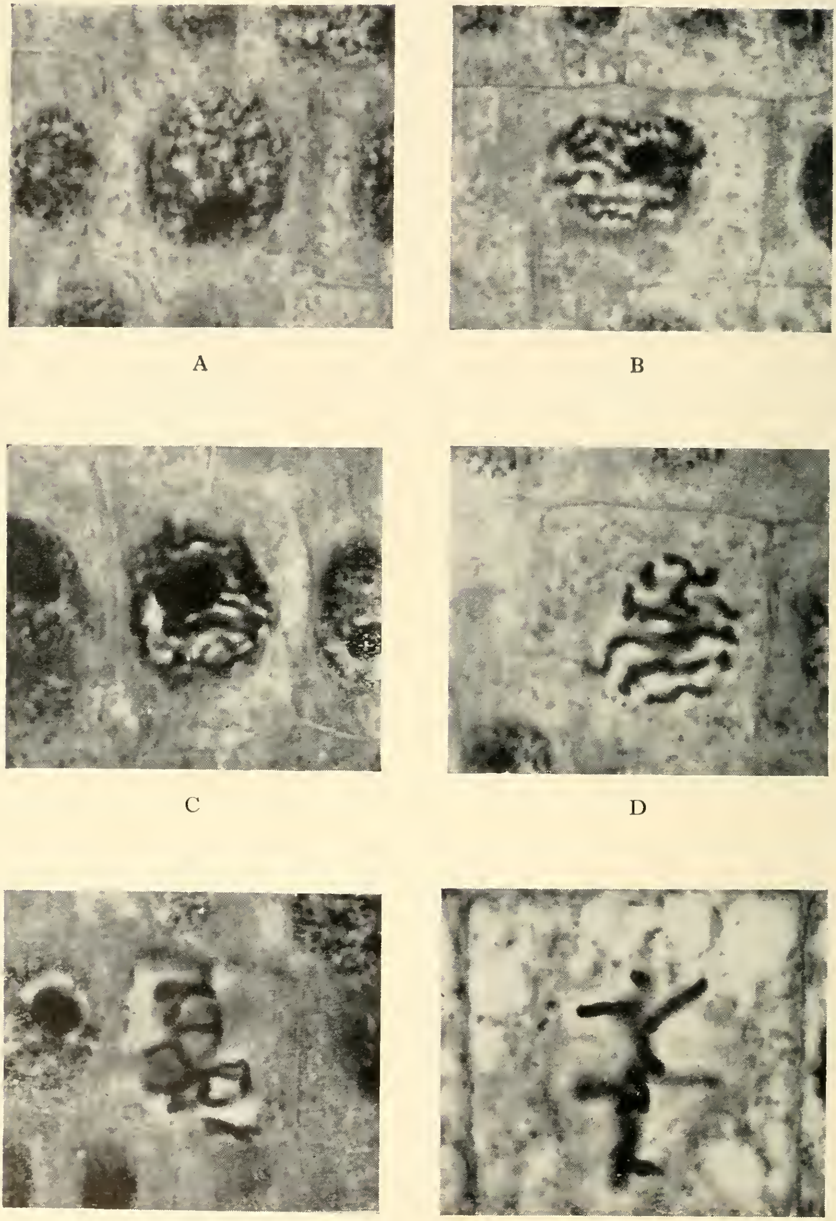
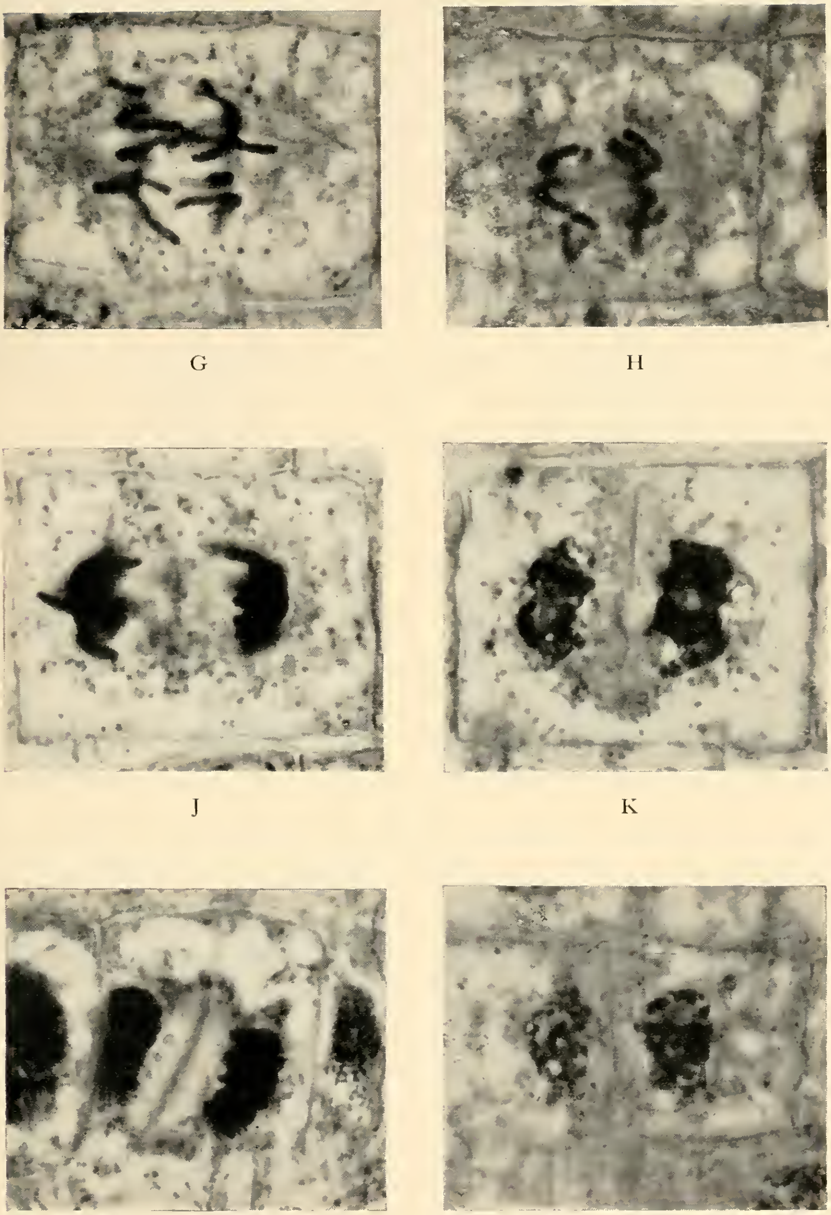


FIG. 10.—*Allium cepa.* Photographs of successive stages of mitosis in cells of the root. A, B, C, D, Stages of the formation of chromonemata in the prophase. E, F, Chromosomes in metaphase.



G H

J K

L M

FIG. 10.—*Allium cepa.* Photographs of successive stages of mitosis in cells of the root. G, H, Chromosomes in anaphase. J, K, Stages of telophase. L, M, Formation of the cell plate. Note the prominent mitochondria in the cytoplasm, especially in the later stages.

any nuclear division and may be given a name or number. Its history can thus be traced through the development of the individual and from generation to generation. There is no escape from the conclusion that the chromosomes are persistent entities, despite the fact that they are not usually recognizable as individuals in the metabolic reticulum, though their persistence in that state may be inferred from the number and distribution of the chromocentres.

It is important to realize that in every diploid nucleus there are two sets of chromosomes, one derived from the male parent and the other from the female. It follows that, in all normal cases, the diploid number of chromosomes must be even. There is thus a pair of chromosomes of each type, called **homologous chromosomes.** Unpaired chromosomes are of exceptional occurrence. In hybrids, in cases where the chromosome complements of the two parents are not identical, some chromosomes may be unpaired, and if there are many of these the cell cannot survive, that is to say, the union of the parents is infertile. In some species there are also unpaired **sex chromosomes,** concerned with the determination of sex. As the single set of chromosomes, derived from one parent, contains the complete set of that parent's genes it is called the **genome.**

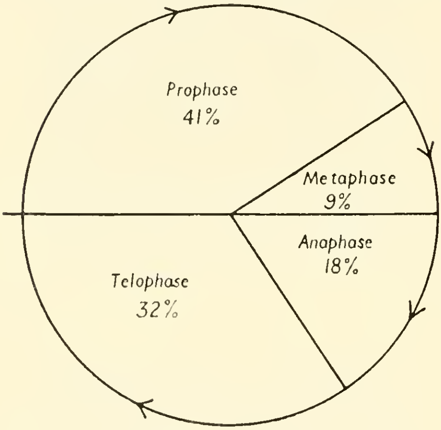


Fig. 11.—Diagram to illustrate the time relationships between the phases in a complete mitotic cycle.

The time relationships of the phases in mitosis are fairly constant, though the total time occupied and also the interval between successive mitoses depend not only on the type of tissue but on external factors such as temperature. Mitosis can be watched in living cells in some cases, such as hair cells or the stigma cells in grasses. In the stigmas of *Arrhenatherum* at 19° C. the total time for the process was found to vary between 80 and 110 minutes. The relative duration of the main phases is shown in the diagram (Fig. 11). Those phases which last longest will obviously be those most often seen in stained preparations.

Cell Division

During telophase spindle fibres remain visible, bridging the space between the daughter nuclei and forming a somewhat barrel-shaped group. Whether they are in fact the same fibres as those attached to the chromosomes, or a newly organized set, is not certain, but the latter is more probable.

Across the equator of this set of fibres a transverse cleavage develops, dividing the cytoplasm and cutting across the fibres. This fissure widens and appears to contain fluid, which soon solidifies as the result of the deposition of pectin, which seems to be the principal substance in the **cell plate** which is thus formed (Fig. 12).

The cell plate first appears in the middle of the cell and extends sideways until it meets the old walls, its extending edge being surrounded by a zone of dense cytoplasm called the **phragmoplast.** Thus a pectic layer grows across the cell, dividing it into two. This layer becomes the **middle lamella** of the new cell wall. Its margin is at first separated from the middle lamella of the parent cell wall by the thickness of the cellulose layer on that wall. The margin of the new membrane thickens and vacuolates, the cellulose wall with which it is in contact breaks down and the vacuolated margin then joins the middle lamella of the old wall, the vacuole becoming part of the intercellular space system and acquiring a lining of pectic substances. Lastly, cellulose layers are deposited on the new lamella, making up a new **primary wall** between the two portions of the divided cell.

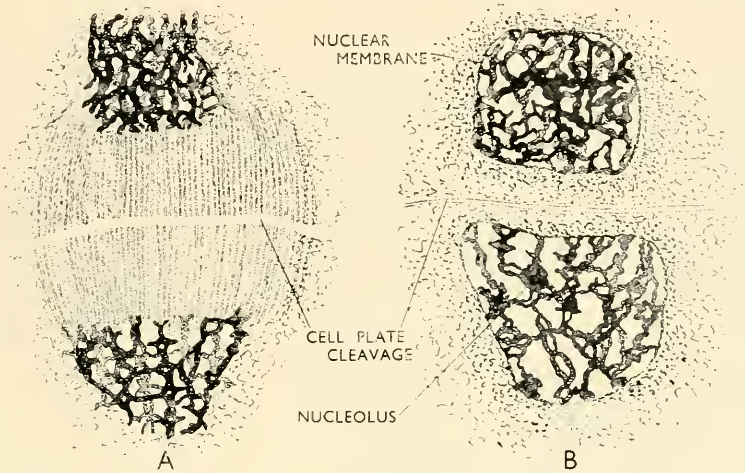


FIG. 12.—*Vicia faba.* Diagram to illustrate two successive phases, A and B, in the development of the cell plate. (*After Fraser and Snell.*)

The spindle fibres disappear when the daughter nuclei obtain their nuclear membranes, but it is possible that a part of them may persist through the new cell wall and form the basis of the **protoplasmic connections** (Fig. 13).

In certain special cases, and especially among lower plants, cell division begins at the periphery of the cell, not at the middle, and a **cleavage furrow** runs inwards towards the centre, closing in like the iris diaphragm of a lens, until the cell is cut in two. The wall material in this furrow is deposited in a manner similar to the above.

Cell division in the higher plants normally obeys certain principles which have been called the **Laws of Cell Division,** though exceptions can be found to each of them in special cases. They are not based upon anything specific to the living cell, but are the expression of physical factors which govern all fluid films, which is in fact the initial state of the cell plate. They are as follows :—

1. Cells normally divide into two equal halves.
2. The plane of the new wall is perpendicular to the direction of maximum growth.
3. The new wall tends to occupy the position of minimal area.
4. The new wall intersects the old walls at right angles, and the line of contact is marked by a minute zone of curvature which makes the old and new surfaces continuous. (The "bourrelet" of Plateau's soap-film experiments.)

The time which elapses between successive divisions of a cell may be looked upon as the duration of a cell generation. This period varies roughly in direct ratio to cell size, though exceptions occur. In Bacteria the period may be only twenty minutes; in larger unicellular organisms such as Diatoms it may be four or five days. The tissue cells of higher plants show correspondingly great variations. The cells of the staminal hairs of *Tradescantia* divide about every eighty minutes at summer temperatures. This is one of the shortest cell generations. At the other extreme are the medullary ray cells of old trees, which can exist without growth or division for periods of up to 100 years.

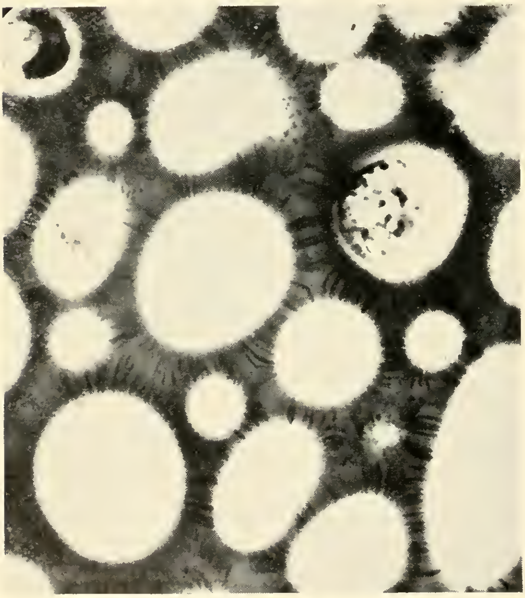


FIG. 13.—*Diospyros sp.* Protoplasmic connections between cells in the endosperm of the seed. The connections appear as darkly stained lines in the thick cell walls.

It is not known what controls the occurrence of cell division. Various explanations have been suggested, such as the decrease in the ratio of surface to volume as the cell grows, or a corresponding reduction in the ratio of nuclear to cell volume. Decreasing viscosity may also be a cause, but it is certain that no single theory by itself is sufficient.

SEXUAL AND ASEXUAL REPRODUCTION

One of the most important characteristics of living organisms is their power of reproducing their kind. Among plants reproduction may take place in a variety of different ways. It is quite common for the simplest plants to multiply by the method of **binary fission,** in which the parent individual splits into two. In others, a small portion of the plant grows out to form a **bud,** which eventually enlarges into a new individual like the parent, from which it may be finally separated. Many plants, too, produce small, round cells, often with a thick resistant coat which withstands adverse conditions. These cells are called **spores,** and under suitable conditions they are detached and develop into new plants.

In all these methods of reproduction only one individual is necessary for the production of a new generation. Such a type of reproduction is called **asexual.** More commonly, however, reproduction is preceded by a **sexual act,** for the purpose of which two individuals or two cells are generally required. The sexual act always includes a fusion of nuclei, which is the essential feature, and generally also the fusion of cells.

In **sexual reproduction** special cells are set apart in the body for the production of new individuals. In all but the lowest types these cells are of two kinds, which we call **male** and **female.** They are often produced in the same individual, but if not, we may distinguish male and female organisms according to the type of cell produced. These special cells are the sex cells, or **gametes.** For reproduction to take place it is necessary for two gametes, one from the male and the other from the female, to come together and fuse completely, forming a fusion cell, or **zygote.** The zygote is the potential new individual.

The male and female gametes are usually unlike in appearance and behaviour. The female gamete is generally a large cell with much cytoplasm and the nucleus is relatively small. As a result of its size this cell is usually non-motile. Such a body is termed an **oosphere.**

The male gamete presents a marked contrast to the oosphere. It is comparatively small, and is usually produced in large numbers. It may consist only of nuclear material and at most it has only a small amount of cytoplasm. In very many plants it is provided with hair-like protoplasmic appendages called **flagella,** by means of which it can propel itself through water. In this way it is able to swim about in search of the female gamete. On coming into contact with an oosphere it has the power of penetrating into the cell, whereupon its nucleus travels through the cytoplasm and fuses with the nucleus of the oosphere. This process is spoken of as **fertilization.** The resulting fusion cell or zygote may rest for a time, but it eventually starts to grow, dividing again and again, and building up an **embryo** or immature individual, which subsequently develops into a new adult form.

Meiosis or Reduction Division

The essential feature of the union of two gametes in the process of fertilization is the fusion of their nuclei. Each of these gametes possesses the **monoploid** or **haploid** (n) number of chromosomes, and hence the zygote will have double the number of chromosomes, that is to say, its chromosome number is **diploid** ($2n$). It follows therefore that, as the chromosome number of a species remains constant, a mechanism must be introduced at some stage in the life-cycle by means of which a reduction or halving of the number of the chromosomes takes place. In animals this generally occurs at the formation of the gametes, but in most plants it takes place in the production of non-sexual spores. The significance of the position of this halving of the chromosome number in relation to the life-cycle will be considered under Alternation of Generations in Volume III.

The mechanism whereby this halving is effected is termed **meiosis,** from the Greek word *meioō* = to lessen. In every diploid nucleus half the chromosomes have been derived from one parent and half from the other parent, and hence we can refer to a maternal and paternal set. It has already been pointed out that in all nuclei the size and shape of the chromosomes differ among themselves, hence in a diploid nucleus the chromosomes all form pairs, and the members of each pair are termed **homologous chromosomes.** In each such pair one member is maternal and one is paternal (Fig. 14).

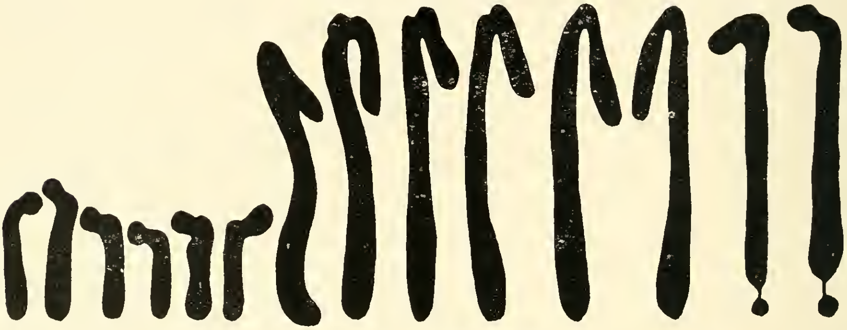


Fig. 14.—*Aloë arborescens.* Complete diploid set of chromosomes showing homologous pairs. (*After Sharp.*)

The essential feature of meiosis as opposed to mitosis is that, in the metaphase of the division, instead of split halves of each chromosome passing to the two poles of the spindle, the homologous pairs of chromosomes unite, then come on to the equatorial plane and separate, so that one whole chromosome of each pair goes to one pole and one to the other. Since it is a matter of pure chance how the chromosomes are arranged at the metaphase, it does not necessarily follow that all the maternal chromosomes pass to the same pole. Usually there is mixing, so that the resulting nuclei contain some paternal and some maternal chromosomes. In no normal case, however, do two homologous chromosomes go to the same daughter nucleus.

Meiosis used to be regarded as involving two separate nuclear divisions which closely followed one another. Since, however, the first is not normally completed before the inception of the second, it is now considered preferable to regard the whole process as continuous but passed through in two stages, resulting in the production of four monoploid daughter nuclei (Fig. 15).

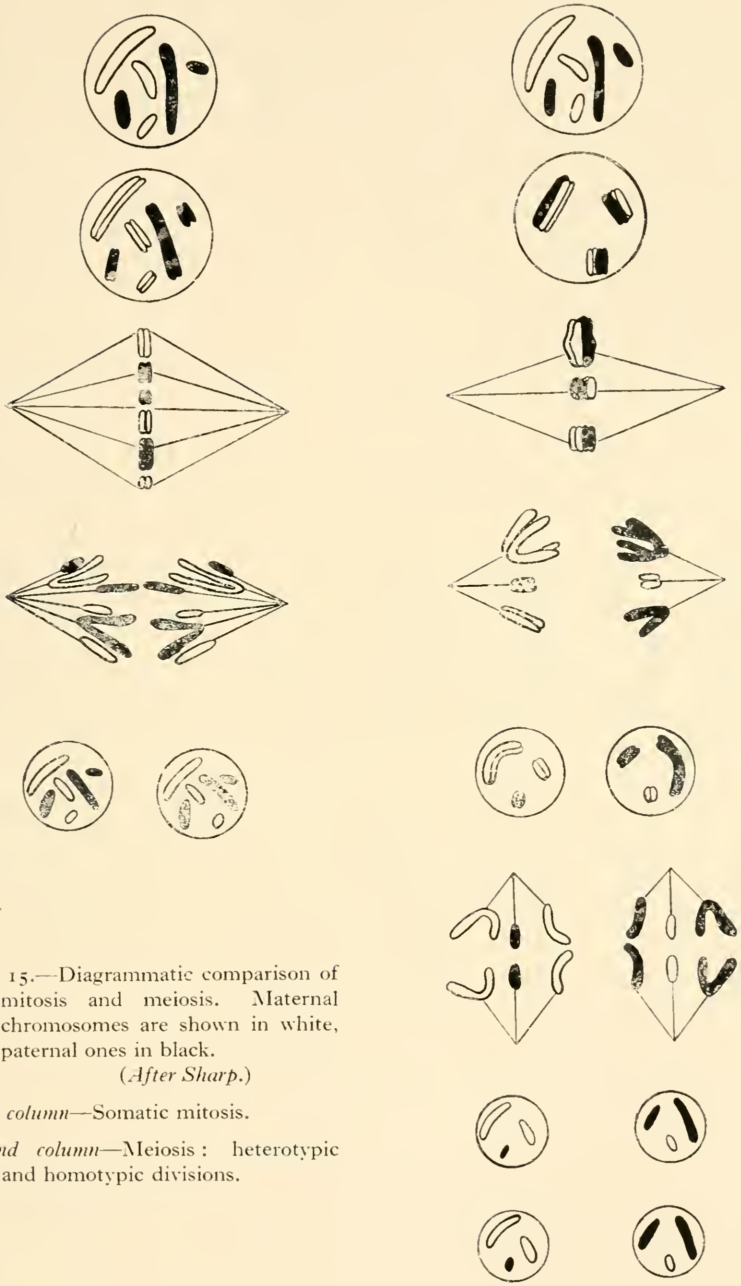


Fig. 15.—Diagrammatic comparison of mitosis and meiosis. Maternal chromosomes are shown in white, paternal ones in black. (*After Sharp.*)

First column—Somatic mitosis.

Second column—Meiosis: heterotypic and homotypic divisions.

The essential features of the process are the following: The first stage, formerly called the **heterotypic division**, begins with the separation from the reticulum of the diploid number of chromonemata. The two members of each homologous pair then come together side by side, the process being known as **synapsis.** This reduces the original diploid number to half that number of **bivalents.**

One member of each pair has been said above to be maternal in origin and the other paternal. Thus, although the members of a pair are homologous in form they differ in hereditary constitution, each corresponding to that of the parent from which it was derived.

The chromonemata on coming together, or sometimes at an earlier stage, split lengthways so that the bivalents comprise a **tetrad** or group of four units called **chromatids.** The four chromatids, lying side by side, may form unions between those of opposite origin at intervals along their length. These are called **chiasmata.**

The matrix now begins to form round the chromonemata, and the resulting bivalent chromosomes contract and thicken until they are much shorter and fatter than any seen in mitosis. At this stage they are scattered throughout the nucleus, an appearance known as **diakinesis.** We now enter metaphase and the bivalents arrange themselves on the equatorial plate ; the spindle fibres appear and the nuclear membrane disappears. The separation that now occurs is not, as in mitosis, the separation of two halves of one chromosome. It is the **disjunction,** *i.e.*, separation, of two whole chromosomes, the paternal and maternal members of the homologous pair which, at synapsis, united to form a bivalent. These now move apart towards the poles of the spindle.

As disjunction occurs the chiasmata that were formed between the units in the tetrad are broken through, so that an interchange of segments takes place between the chromonemata involved. This exchange of paternal and maternal material is known as **crossing over** (Fig. 16), and it implies a redistribution of hereditary material which is of the highest genetical importance.

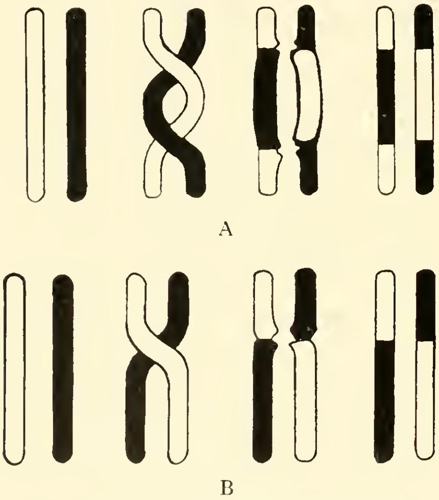


Fig. 16.—Diagram to illustrate the formation of chiasmata in unsplit homologous chromosomes. (*After Sharp.*)

It will be recollected that when the homologous pairs came together the chromonemata split, so that each chromosome which now disjoins contains two chromonemata or, with the adherent matrix, two chromatids. As anaphase progresses the matrix on the chromosomes diminishes and the double internal thread becomes visible again.

When the chromosomes reach the spindle poles they retain their individuality until the second stage, or **homotypic division,** commences. Two achromatic spindles are formed in the cell at right angles to the first, in such a position that their equators coincide with the poles of the heterotypic spindle. In this way the anaphase of the heterotypic division passes directly into the metaphase of the homotypic division. The chromosomes now split longitudinally as in mitosis, the two halves pass to opposite poles, and the subsequent stages follow the same sequence as in ordinary nuclear division, the final result of the whole process being the reformation of four monoploid nuclei. This is usually followed by the formation of four cells, though all may not necessarily survive. These monoploid cells mark the beginning of a new phase in the cytological cycle of the life history in the organism concerned, and they normally function as reproductive cells, beginning also a new generation. Whether they act as non-sexual spores and germinate directly, or whether they function as gametes which only germinate after conjugation, depends on the type of alternation of generations which the organism displays, but in plants the former is universal outside the Thallophyta.

Chromosome Numbers of Types Described in this Textbook *

ALGAE

Chlamydomonas spp.	20	*Vaucheria terrestris*	20
Spirogyra spp.	24	*Cutleria multifida*	48
Pandorina morum	24	*Dictyota dichotoma*	32
Eudorina elegans	20	*Fucus serratus*	32
Volvox aureus	24	*Batrachospermum moniliforme*	20
Oedogonium spp.	38	*Polysiphonia violacea*	40
Cladophora glomerata	30-32	*Corallina officinalis*	48

FUNGI

Myxomycetes (*most spp.*)	16	*Erysiphe communis*	16
Plasmodiophora brassicae	16	*Rhytisma acerinum*	8
Mucor hiemalis	4	*Peziza vesiculosa*	16
Cystopus candida	24-32	*Puccinia graminis*	4
Sphaerotheca castagnea	8		

LICHENES

Peltigera canina	4

CHAROPHYTA

Chara fragilis	48

BRYOPHYTA

Pellia epiphylla	16	*Mnium hornum*	12
Marchantia polymorpha	16	*Polytrichum commune*	12-14
Anthoceros laevis	8	*Sphagnum squarrosum*	40

PTERIDOPHYTA

Lycopodium clavatum	28	*Psilotum triquetrum*	96-104
Equisetum arvense	56-230 ?	*Dryopteris filix mas*	144
Isoetes spp.	22	*Pteridium aquilinum*	64

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* The diploid number is given in each case. Where the number varies considerably it probably indicates that the higher number is that of a polyploid.

GYMNOSPERMAE

Cycas revoluta	24	*Ephedra distachya*	24
Ginkgo biloba	24	*Gnetum gnemon*	24
Pinus sylvestris	24	*Welwitschia mirabilis*	50 ?
Taxus baccata	16-24		

ANGIOSPERMAE (Selected)

Crepis capillaris	6	*Convallaria majalis*	38
Ranunculus acris	14	*Senecio vulgaris*	40
Bellis perennis	18	*Cerastium vulgatum*	144
Quercus robur	24	*Rumex hydrolapathum*	200

OUTLINE OF THE HISTORY OF CYTOLOGY

Cytology is one of the most actively advancing branches of biological study and we are far from having reached even an adequate knowledge of the working of cell processes, so that our descriptions must be regarded as tentative and our interpretations of them as more tentative still. Yet, when we look back over the last century we see that cytology has advanced through certain well-defined stages, each marked by the recognition of some basic fact, which has proved itself a starting-point for further discovery. This is the touchstone of validity in science, that a discovery or a theory should prove fertile in new discoveries. Viewed in this light we may note the following phases of advance :—

1. Robert Brown in 1831 discovered the existence of nuclei in cells. This may be said to have been the first discovery of importance in cytology since cells were first observed by Hooke in the seventeenth century.

2. In 1846 came the recognition of cytoplasm as a characteristic of living cells by von Mohl.

3. In 1848 Wilhelm Hofmeister first observed that the cell nucleus may resolve itself into microscopic rod-like bodies. Although he attached no interpretation to the discovery, we may regard this as the discovery of the chromosomes. He also discovered the nuclear membrane and the nucleolus and observed their disappearance at nuclear division. Lastly, he discovered the cell plate which becomes the new cell wall.

4. Flemming and Strasburger in 1882 (Fig. 17) observed the splitting of the chromosomes during division, and van Beneden ascertained that the split halves are accurately distributed to the two daughter nuclei. Thus the process of mitosis was clearly defined.

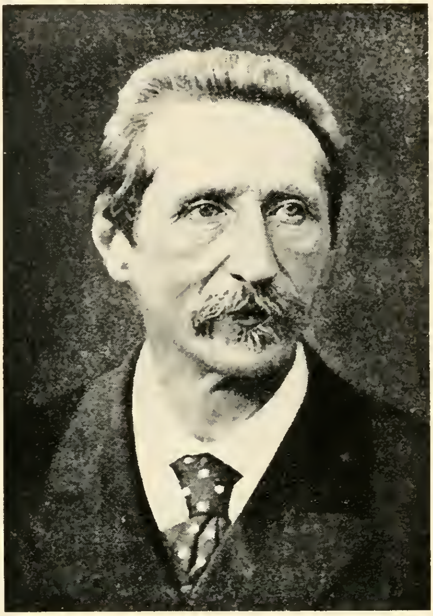
5. Van Beneden in 1883 and Strasburger in 1888 discovered the reduction division which is associated with sexual reproduction, and showed that sexual conjugation is essentially the union of two reduced nuclei to form one, which has double the number of chromosomes. This established the existence of the cytological phases of the life-cycle, and the importance of the nuclear substance as the material of heredity.

6. In 1883 van Beneden came to the conclusion that chromosomes had a permanent individuality, but this belief did not find a proof till much later.

Boveri, however, in 1909 succeeded in demonstrating it, and since then others have augmented his proof, so that the way was open for the recognition of the chromosomes as permanent hereditary units.

7. Roux in 1883 and Weismann in 1887 had supported the idea that the units of inheritance were arranged in a linear order in the chromosomes, a view which fitted in with the process of longitudinal splitting in division. This found a modern expression in the theory of the " Genes " as the hereditary units in the chromosomes, proposed by Morgan in 1926. Cytological proof of this theory is very recent, but it has been strongly supported by genetical work on the Fruit Fly, *Drosophila*, which has enabled investigators to identify the positions of many such genes on particular chromosomes.

8. This brings us to the last and most recent of the basic concepts in cytology, namely that each chromosome pair carries a group of associated hereditary characters (linkage groups) and that these may be exchanged between them by crossing-over during meiosis.



[*Courtesy of the Linnean Society.*

FIG. 17.—Portrait of Edouard Strasburger.

It is impossible to separate sharply between cytology and genetics at the present time, for the two branches of the science have become closely bound up with one another. In earlier times cytology and genetics travelled along separate paths, and it was not till 1887 when Weismann put forward his theory of the " Inheritance of the Germ Plasm " that the union of the two branches became established. From that time onwards they have become increasingly united. It follows therefore that it has been impossible in this chapter to separate sharply cytology from genetics, and the student is advised to read this chapter in conjunction with the account of genetics given in Volume IV.

SUMMARY OF THE BASIC IDEAS IN CYTOLOGY

1. Every organism consists of cells. These possess, normally, a **cell wall,** a colourless semi-liquid material **cytoplasm,** and a **nucleus,** both the latter constituting the **protoplasm** or living substance. In addition the cell may include **plastids,** which often bear pigments, *e.g.*, **chloroplasts.** These are embedded in the cytoplasm. The cytoplasm contains immense numbers of minute granules of substances formed by it and also larger units, rod-like

or granular, called **mitochondria.** In the cytoplasm are usually spaces, the **vacuoles,** empty in appearance but filled with cell-sap. They may coalesce into a single large vacuole filling the central part of the cell.

2. The nucleus consists of a **nuclear membrane,** enclosing a limpid, semi-solid material, the **karyolymph.** In this is suspended a hollow

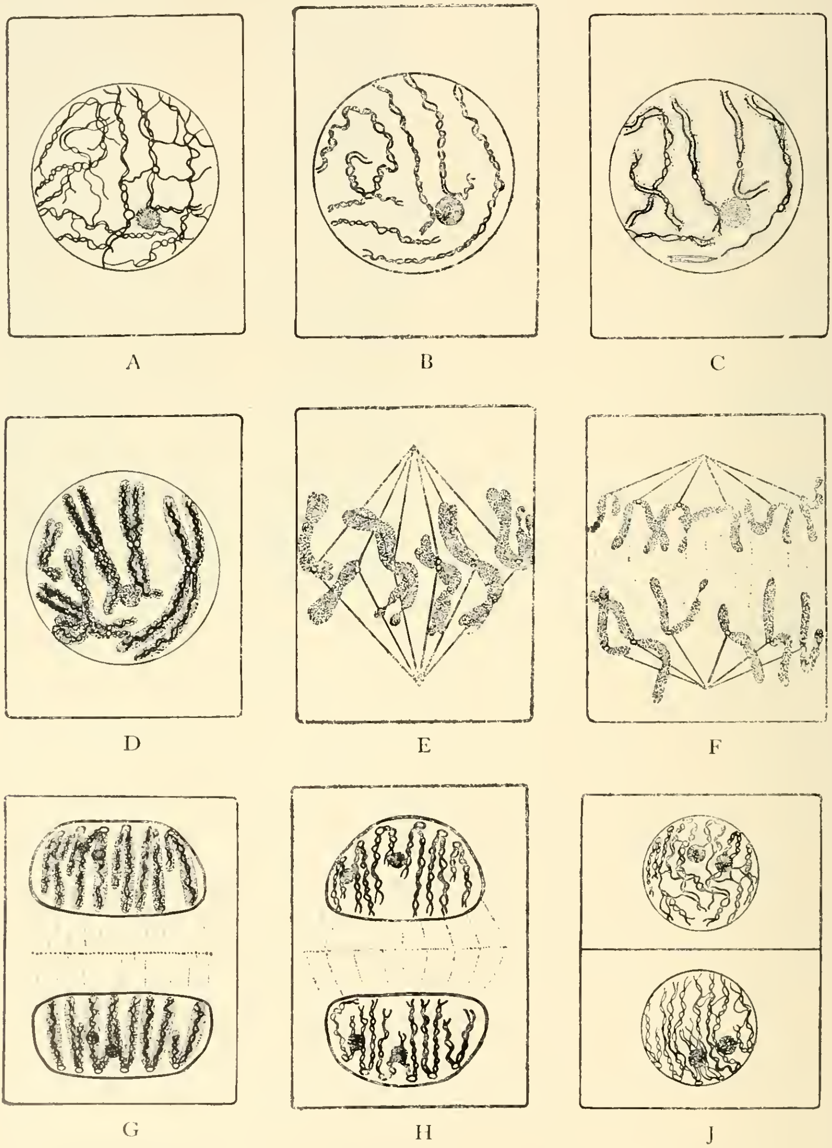


FIG. 18.—Diagram of somatic cell division. A, B, C, D, Stages of prophase showing the formation of chromonemata and chromosomes. E, Metaphase. The spindle fibres are shown attached to the kinetachores of the divided chromosomes. F, Anaphase. The diaster stage. G, H, J, Stages of telophase showing the reconstruction of the nucleoli and the formation of the new cell wall. (*After Sharp.*)

reticulum composed of **chromatin.** In this network are numerous knots or lumps of **heterochromatin.** Attached to the reticulum are one, or sometimes two, **nucleoli** which differ from the chromatin in composition.

3. Cell division is preceded by nuclear division or **mitosis.** The reticulum is resolved into a number of separate threads, whose number is fixed and characteristic for each species. These threads thicken and are called **chromosomes.** Each of them has a distinctive shape or size. They split lengthways, and the portions or **chromatids** separate and move to opposite ends of the cell, where they reconstitute two daughter nuclei. The chromosomes are drawn apart by two sets of cytoplasmic fibrils called the **spindle fibres,** which appear only during nuclear division. The nucleolus and the nuclear membrane disappear in the early stages of division and are reformed at its conclusion. Between the daughter nuclei a **cell plate** is formed, which becomes a new cell wall (Fig. 18).

4. Sexual reproduction consists essentially of the union of two nuclei, one from each of the parents. Thus after fusion the nucleus contains two sets of chromosomes, each pair of the same type forming what is called an **homologous pair.** As this would inevitably lead to a progressive doubling in the number of chromosomes, from generation to generation, there is a periodic halving or **meiosis** of the chromosome number. The sexual nuclei have always the half number (**monoploid**), and their union re-establishes the double number (**diploid**).

5. The special **reduction division** or **meiosis** does not always occur at the same point in the life-cycles of different organisms, but it is always associated with the formation of some type of reproductive cell, either sexual or non-sexual. Even in the latter case, which is common in plants, it may be regarded as a preparation for eventual conjugation. The process of reduction division involves two immediately successive nuclear divisions, resulting in the formation of a quartet of cells. In the first division (**heterotypic**) the chromosomes of homologous pairs unite together and then disjoin, each chromosome being then separated to form part of a daughter nucleus. In other words, at this stage *whole chromosomes are segregated* instead of halves as in mitosis. The two daughter nuclei thus contain half the number of whole chromosomes. In the second division (**homotypic**) each of these chromosomes splits, as in mitosis, followed by separation as before. The final result is four nuclei each with the reduced number of chromosomes.

CHAPTER III

THE BASIS OF PLANT CLASSIFICATION

THE SPECIES

IN any scheme of botanical classification the ultimate basis must be the individual organisms. But many individuals resemble each other so closely that we instinctively recognize that they form natural groups or **species.** It is important to realize that the idea of species arises from our natural intuition and not from scientific definition.

A child collecting flowers by the wayside can usually tell without difficulty how many kinds he has found, and these, generally speaking, will correspond to the different species recognized and defined by the botanist. A species then, may be said to represent the empirical unit of botanical classification.

Even among the higher and better-known plants, however, many of the so-called species are not sharply distinguishable from one another and we find intermediate forms or connecting links, which can only with difficulty be referred to either of two closely similar species. Among the lower plants this difficulty becomes even greater, for the individuals which comprise the species not only present fewer points for comparison but they vary considerably according to the environmental conditions under which they are growing. The more we study plants the more clearly we realize that had we all the past and present individuals before us it might be impossible, except in an arbitrary manner, to arrange them in species at all, for each kind would be found to be connected with others by a series of gradations.

Our interpretation, then, of a species must be to some extent an arbitrary one, and botanists often disagree as to the extent of the variation in form which may be admitted within any one species. For example, a common weed, Whitlow grass (*Erophila verna*) (Fig. 19), regarded by Linnaeus as constituting a single species, occurs under something like a hundred * forms, separated by minute but constant differences, which some accept as distinct species. In general, botanists may be said to be divided into two camps, the " lumpers " and the " splitters " ; the former endeavouring to keep the number of species as few as possible, the latter dividing each species up into ever-increasing numbers of sub-species and varieties.

For purposes of classification it is not sufficient merely to group all the individual plants into species. These species must in turn be collected together in groups of a higher order which are termed **genera.** The genera are grouped together in **families,** and the families in turn are assembled in **orders,** each group having certain characters in common. In this way a system of classification is built up in which the orders are grouped in **classes,** classes in **phyla,** and the phyla into **kingdoms.** Of these kingdoms only

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* Modern cytological research has greatly reduced this number.

two are generally recognized—the plants and the animals—and even they cannot be sharply separated from each other, for the simplest plants and the lowest animals differ but little.

Every species, genus, family and so on is defined botanically by what is called a **diagnosis**, generally written, for the sake of precision, in Latin, giving in general terms a description of the characters common to the organisms or groups of organisms which are to be included in the assemblage, and no additional individual or group can be included unless it conforms to the diagnosis of the group into which it is placed.

FIG. 19.—*Erophila verna.* A number of micro species included in the Linnean species. (*After Jordan.*)

The arrangement of individual organisms into species, and the grouping of these into genera, families and so on, constitutes the work of the **systematist**, and is usually spoken of as **classification**; whilst the study of the principles in accordance with which the classification should be carried out forms the special branch of biology spoken of as **taxonomy**.

HISTORY OF CLASSIFICATION

The history of classification was for many centuries the history of Botany. The earliest interest of man in plants was entirely in their usefulness to him, either as food, as medicine or as magical charms. In endeavouring to convey such knowledge to others, descriptions of species had to be framed, and it was inevitable that simple ideas of classification should arise out of the work of description, such, for example, as the notion of the species and the grouping of plants in general into trees, shrubs, herbs, grasses etc., according to their habit of growth. From time immemorial certain plants were cultivated or were sought in the wild state, and familiarity with their habits gave rise to primitive ideas on plant physiology, which remained almost unchanged until the eighteenth century. Classification, on the other hand, began to make advances at the beginning of written history about the fifth century B.C. This period was one of those recurrent epochs of activity in which men's minds become deeply stirred by new ways of thought, and it was signalized by the appearance for the first time of great teachers who had theories to expound.

Part of this activity was medical and resulted in a great extension of information about plants, which must have rendered evident the need for systematization. Accordingly in the fourth century B.C. we find Aristotle (384-323 B.C.) using the resources placed at his disposal as the tutor of Alexander the Great to make extensive collections and to begin the work of arrangement on logical lines. Aristotle was not principally a botanist, though he wrote a book, now mostly lost, on plants. The real founder of botanical science was Theophrastus of Eresus (371-285 B.C.), who was taught by Aristotle and succeeded him as teacher at the Lyceum. His outlook, like that of his predecessor, was thoroughly scientific. He deliberately formulated scientific problems, stating them in clear language and endeavouring to solve them by intellectual means. The distance between such an objective philosophy and primitive utilitarianism marks one of the greatest advances in human culture.

The downfall of Grecian liberty put an end to this great period and the next names we must mention are those of Romans. Pliny the Elder (A.D. 23-79) was imbued with the Greek tradition of inquiry, but lacked the critical and sceptical attitude of the old Greeks. His " Natural History " is an enormous compilation of material, largely from other authors, which preserved for later ages some part of the lost learning of antiquity. It exercised the greatest influence on medieval natural philosophy, and was not displaced until Aristotelean originals became available in the thirteenth century.

Another Roman botanist was Dioscorides (first century A.D.), a native of Asia Minor and a physician. He was therefore in the intellectual succession from the Greek herbalists of the fifth century B.C., and his work was medical and practical in intention. Nevertheless his book, which was encyclopaedic for his time, remained until the Renaissance the chief storehouse of botanical information, and it exercised a great influence on the botanical studies of the Middle Ages. In spite of the purely practical aim of the work its methodical treatment showed the way towards scientific system.

Throughout the early Middle Ages there is nothing to record but a series of commentaries on the antique authors, becoming more and more corrupted and ignorant as time went on. The urge of intellectual curiosity was away from Nature towards the spiritual and the unseen. Theology, logic and rhetoric reigned supreme in the medieval mind, while the study of Nature was confined to inferior minds whose objects were wholly utilitarian.


Fig. 20.—Portrait of Andrea Cesalpino.

Fig. 21.—Portrait of John Gerard, taken from the title page of his "Great Herbal."

The first break in the clouds came with Albert von Böllstadt (1193-1280), known as Albertus Magnus, "Doctor Universalis," a man of great eminence whose chief claim to our notice as a botanist was that he reintroduced the study of Aristotle in preference to Pliny, and so brought back the idea of objective reasoning into natural science. Not until the Renaissance, however, did this bear fruit, when Andrea Cesalpino (1519-1603) (Fig. 20) produced the first work of modern times which can be called truly scientific, in that he once more set out to discover a reasoned classification of plants which had a purely intellectual purpose. From him we may date scientific classification as a study, and he was directly inspired by the Aristotelean philosophy. Botany as a science now parts company with the medical study of herbs. We must mention, however, the company of herbalists, contemporaries of Cesalpino, who, although they marked no philosophical advance, imbued botanical study with the Renaissance principle of first-hand inquiry. They belonged to various nations, and we need only mention Brunfels (1464-1534), Fuchs

(1501-66), Dodoens (1517-85) and Clusius (1526-1609). The "Herbals" produced by these men were notable for their freshness of outlook, and especially for their accuracy of description and fidelity of illustration. Among them we should also rank William Turner (1515-68), who was the first to publish a herbal in English with references to British plants. He was closely followed by John Gerard (Fig. 21) (1545-1612), whose "Great Herbal" remained for generations the most popular book of Botany in these islands.

Fig. 22.—Portrait of Kaspar Bauhin.

Herbals have an interest for others besides botanists. In the early days of printing they were the only fully illustrated books, and thus they are the most important documents in the history of the art of illustration. They also provide a mine of material for designers, and it is a fact that many of the traditional floral designs used in the Arts can be traced back to the herbals of Dioscorides (Matthiolus' edition, 1583), Fuchs and Dodoens.

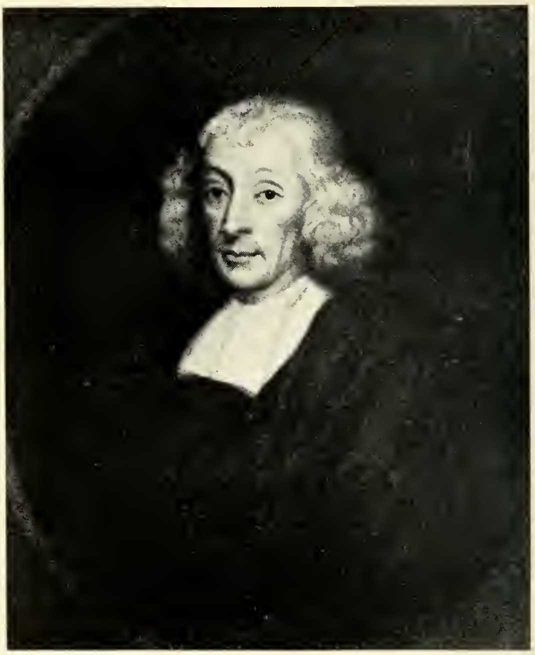


Fig. 23.—Portrait of John Ray.

Although these later herbalists were not primarily interested in classification they were led towards it inescapably through their labours of description. The idea of affinity made itself unconsciously felt, and broad classes such as Fungi, Mosses, Conifers, etc., began to appear, though not based upon any philosophical concept.

Cesalpino was soon followed by other authors, notably Kaspar Bauhin (1560-1624) (Fig. 22), who wrote several books of plant description in which he attempted a classification by natural affinities rather than by logical reasoning, a notable step towards a truly natural system. He also first clearly grasped the idea of a Genus, and he invented the principle of binomial nomenclature, which, however, he did not apply universally. His best-known work, the "Pinax Theatri Botanici," is one which is still a valuable authority on the early history of nomenclature.

FIG. 24.—Portrait of Carl von Linné.

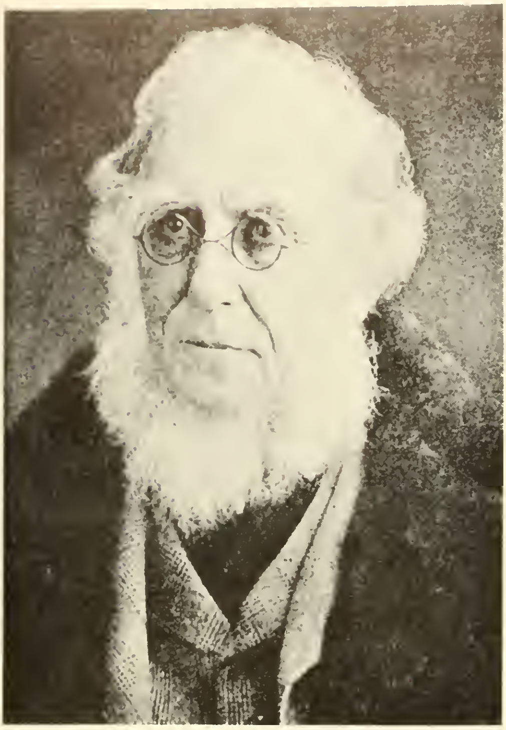
With the seventeenth century we enter a period in which classification was definitely sought by all botanical authors as the primary necessity of the science. Unfortunately the idea of natural affinities was overlaid by the desire to form a symmetrical and logical classification which would appeal to the mathematical spirit of the age. Hence we now group all these earlier efforts together as "artificial classifications" because all the weight was laid upon one character, which was deemed by the author to be the most important and was rigidly utilized, in violation very often of clear natural associations.


[*Courtesy of the Royal Horticultural Society.*

FIG. 25.—Portrait of Professor John Lindley.

This period lasted from Bauhin to Linnaeus, that is, for about a century, during which several treatises of great learning were produced, still valuable in detail, although their systematic basis was ineffective. We may mention Tournefort (1650-1708) and Rivinus (1652-1725), who based their classifications on the corolla; and especially John Ray (1628-1705) (Fig. 23) and Robert Morison (1620-83) in England, who used the fruit as a distinguishing mark. Of these Ray was the greatest naturalist. He had clearly the idea of a natural system in his mind but was unable to produce it himself. Indeed it was an impossibility at the time for lack of information.

These men paved the way for



[Courtesy of the Linnean Society.

FIG. 26.—Portrait of Sir Joseph Hooker.

Linnaeus (Carl von Linné) (Fig. 24), the great Swedish botanist (1707-78), one of the greatest systematizers in science. That he was not unaware of his own pre-eminence is shown by his proud motto, "Deus creavit, Linnaeus disposuit." * His immediate influence on the science of his own day was due to his skilful "sexual system," an artificial system, quite in the seventeenth-century tradition, based upon the number of stamens and carpels in the flower. It was much more successful than any of the previous attempts of the kind and became widely popular. Linnaeus, himself, however, was fully aware of the need for a natural system, though he, like Ray, was unable to produce more than the skeleton of such a system. He left a list of sixty-five families, many of them with their present-day names, which he declared to be, in his opinion, natural, but he was unable to find definite rules of evidence for deciding the matter and owned that, for the time being, such a system rested on nothing more than instinctive feeling.

The more enduring service of Linnaeus was his adoption of binomial nomenclature as a positive rule and his thoroughgoing application of it in his "Species Plantarum," 1753, in which he revised nomenclature according to the new method. This marks an epoch in systematic botany, and it is taken as the official starting-point from which all priority in nomenclature is reckoned. Earlier names, unless adopted by Linnaeus, were all dropped.

[Courtesy of the Linnean Society.

FIG. 27.—Portrait of Robert Brown.

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* "God created, Linnaeus arranged."

The founder of the natural system, as something completely distinct from artificial systems, was Antoine Laurent de Jussieu (1748-1836), who described and gave characters to a hundred families, nearly all of which are still recognized. His uncle Bernard illustrated these ideas in laying out the gardens of the Petit Trianon for Queen Marie Antoinette.

From the principles laid down by de Jussieu systematic botany has never departed. The work of the great nineteenth-century systematists was built on his foundation, but it elaborated and extended the system as exploration vastly increased our knowledge of plants. We should mention especially John Lindley (1799-1865) (Fig. 25), who established Kew Gardens as a national possession, and Sir Joseph Hooker (1817-1911) (Fig. 26), author of a series of great Floras of the British Dominions, who, with George Bentham, also set to work to rescue the genera of flowering plants from the confusion into which they had fallen. Their work, the " Genera Plantarum," remains the foundation work for all generic definitions.

New versions of the natural system have appeared from time to time, embodying current conceptions of affinity. Among the most notable we must mention that of Adolf Engler which was embodied in his great work, edited in collaboration with Prantl, " Die Natürliche Pflanzenfamilien."

It becomes invidious to attempt to select names from among the great multitude who have contributed to build up modern knowledge of systematics, and we can only cite a few whose work was of a fundamental nature. Pyramus de Candolle (1778-1841), who developed the principles of natural classification in a series of classic monographs ; Robert Brown (1773-1858) (Fig. 27), who first separated the Gymnosperms as a group ; Asa Gray (1810-88), the great systematist of the North American Flora ; and lastly a number of men, each of whom was associated particularly with one of the groups of the lower plants : Sir William Hooker (1785-1865) with the Ferns ; C. H. Persoon (1762-1836) and Elias Fries (1794-1878) with Fungi and Lichens ; P. A. Saccardo (1845-1920), author of the monumental " Sylloge Fungorum " ; J. Hedwig (1730-99) with the Bryophyta ; and W. H. Harvey (1811-66), K. H. Agardh (1785-1859) and de Toni (1864-1924) with the Algae.

It is impossible to follow developments into recent times, and, indeed, it is worth comment that as science progresses the importance of personality tends to fade into the background and to be replaced by the dominance of theories which become the most influential factors in the advance of knowledge.

Principles of Classification

We have referred above to the application by Linnaeus of the system of **binomial nomenclature.** This consists of giving every organism two names : a **generic name** and a **specific name.** The generic name is used to describe forms which bear a general similarity to one another, for example, the pear, the apple and the mountain ash are all placed in the same genus, *Pyrus.* The specific name distinguishes the members of the genus from one another, the pear being *Pyrus communis* ; the apple, *Pyrus malus* ; and the mountain ash, *Pyrus aucuparia*. Thus we see that the generic name becomes comparable with the surname in human society, while the specific name is equivalent to the Christian name.

In order to assist in appreciating the rank of various terms it is customary that all names of Families should end in **-aceae** and those of Orders in **-ales,** while Sub-orders end in **-ineae.** The names of Phyla should end in **-phyta.** Unfortunately this system has been adopted relatively recently and some of the older names do not fit properly into the scheme, so that there are many exceptions to these terminations.

As knowledge increases there is a tendency to separate and differentiate organisms in an ever-increasingly complex system. Critical work on any group generally results in splitting up the species into a larger number and as a result classification becomes more complicated. Moreover authorities often differ as to the importance to be attached to particular features and as a result their systems of classification vary.

We are concerned here, however, with the main outlines of plant classification, and about these substantial agreement exists. The following scheme therefore is one which is generally accepted among botanists and it offers a comparatively simple arrangement of the more important groups. Much has been left out intentionally for the sake of simplicity, and only those orders are mentioned of which a particular type will be subsequently considered in detail in this book.

OUTLINE OF THE CLASSIFICATION OF PLANTS *

1. **Thallophyta.** Plant body a thallus, with no distinction of stem, root and leaf. Individuals mostly small with simple organization, many microscopic.

(*a*) ALGAE. Organisms possessing chlorophyll and sometimes additional pigments.

(1) *Euglenophyceae.* Motile protoplasts with no cellulose wall. No sexual reproduction.

(2) *Chlorophyceae.* Cellulose wall present. Chlorophyll only. Fresh-water and marine.

(3) *Cyanophyceae.* Blue-green colour due to phycocyanin. Fresh-water and marine.

(4) *Phaeophyceae.* Brown colour due to fucoxanthin. Exclusively marine.

(5) *Bacillariophyceae.* Unicellular forms with silicified cell walls. Brown colour due to diatomin. Fresh-water and marine.

(6) *Rhodophyceae.* Red colour due to phycoerythrin. Predominantly marine.

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* A full discussion of the methods and principles of plant classification will be included in Volume II.

(*b*) FUNGI. Organisms devoid of chlorophyll ; either saprophytic or parasitic.

(1) *Archimycetes.* Thallus a naked mass of protoplasm. Asexual reproduction by spores formed in sporangia. Sexual reproduction by motile gametes.

(2) *Phycomycetes.* Thallus a mycelium of non-septate hyphae. Asexual reproduction by spores formed in sporangia, or by conidiospores. Sexual reproduction by variously formed gametes.

(3) *Ascomycetes.* Mycelium of septate hyphae. Asexual reproduction by conidiospores. Sexual reproduction resulting in ascospores formed in sac-like cells (asci) which form a fruiting body.

(4) *Basidiomycetes.* Mycelium of septate hyphæ. Asexual reproduction occasionally by conidiospores. Sexual reproduction resulting in basidiospores borne on short stalks from special cells (basidia) developed on a fruiting body.

(*c*) BACTERIA. Minute unicellular organisms, usually devoid of chlorophyll and without a fully organized nucleus. Reproduction by binary fission and by spores. Sexual reproduction doubtful.

(*d*) LICHENES. Compound organisms consisting of fungal and algal partners. Reproduction fungal (mostly Ascomycetes).

2. **Charophyta.** Thallus jointed, branched, attached at the base ; consisting of large coenocytes, containing chlorophyll. Sexual reproduction by antherozoids in antheridia and oospheres in oogonia. Fresh-water.

(*a*) CHARALES. The sole order. Characters as above.

3. **Bryophyta.** Terrestrial or fresh-water. Gametophyte either a thallus or differentiated into stem and leaves, attached by rhizoids but without true roots. Sexual reproduction by antherozoids in antheridia and oospheres in archegonia. Sporophyte permanently attached to the gametophyte. Homosporous.

(*a*) HEPATICAE. Gametophyte thalloid or with leafy stem. Sex organs apical or dorsal. Sporophyte usually non-chlorophyllous.

(*b*) MUSCI. Gametophyte with leafy stem. Sex organs apical or lateral. Sporophyte usually chlorophyllous.

4. **Pteridophyta.** Mainly terrestrial. Sporophyte with stem, roots and leaves. Vascular tissue present. Spores produced in sporangia. Gametophyte a small prothallus bearing antheridia and archegonia.

(*a*) PSILOPSIDA. Sporophyte with small leaves (microphyllous) or none. Homosporous. No true roots. Sporangia free or united into synangia, terminal or on specialized branches. Gametophyte in living forms reduced, saprophytic.

(*b*) Lycopsida. Sporophyte with numerous, usually small leaves (microphyllous). Homosporous or heterosporous. Sporangia free, borne on or axillary to sporophylls. Gametophyte reduced, saprophytic or enclosed in the spores.

(*c*) Sphenopsida. Sporophyte with jointed stems and small leaves in whorls (microphyllous). Homosporous. Sporangia clustered, in terminal strobili. Gametophyte green.

(*d*) Pteropsida. Sporophyte with large leaves (megaphyllous). Homosporous or heterosporous. Sporangia clustered on foliar organs. Gametophyte either green, or reduced and enclosed in the spores.

5. **Spermatophyta.** Sporophyte with stems, roots and leaves. Vascular tissue present. Heterosporous. Microspores (pollen grains) and megasporse (embryo sacs) produced in distinctive sporangia. Megasporangia with integuments, developing into seeds. Gametophytes extremely reduced, enclosed in the spores.

(*a*) Pteridospermae. Leaves fern-like. Sporangia borne on normal or only slightly reduced leaves, not aggregated into flowers.

(*b*) Gymnospermae. Sporangia aggregated into strobili (cones), each usually containing only one type of spore. Megasporangia exposed.

(*c*) Angiospermae. Sporangia either in separate or in the same flowers. Megasporangia enclosed in carpels, which ripen into fruits.

- (1) *Dicotyledons.* Embryo with two cotyledons. Leaves mostly net-veined.
- (2) *Monocotyledons.* Embryo with one cotyledon. Leaves mostly parallel-veined.

OUTLINE CLASSIFICATION OF TYPES DESCRIBED

THALLOPHYTA

A. Algae.

(i) *Euglenophyceae.*	
Euglenales.	*Euglena.*
(ii) *Chlorophyceae.*	
Volvocales.	*Chlamydomonas*, *Haematococcus*, *Gonium*, *Pandorina*, *Eudorina*, *Volvox.*
Chaetophorales.	*Pleurococcus*, *Coleochaete.*
Ulotrichales.	*Ulothrix.*
Oedogoniales.	*Oedogonium.*
Conjugales.	*Spirogyra.*
Siphonales.	*Bryopsis*, *Vaucheria.*
Siphonocladiales.	*Cladophora.*
(iii) *Cyanophyceae.*	
Hormogoneales.	*Nostoc.*

(iv) *Phaeophyceae.*	
Ectocarpales.	*Ectocarpus.*
Cutleriales.	*Cutleria.*
Dictyotales.	*Dictyota.*
Laminariales.	*Laminaria.*
Fucales.	*Fucus.*
(v) *Bacillariophyceae.*	
Pennales.	*Pinnularia.*
(vi) *Rhodophyceae.*	
Nemalionales.	*Batrachospermum.*
Gigartinales.	*Chondrus.*
Ceramiales.	*Polysiphonia, Ceramium.*
Cryptonemiales.	*Corallina.*

B. FUNGI.

(i) *Archimycetes.*	
Myxomycetales.	
Plasmodiophorales.	*Plasmodiophora.*
(ii) *Phycomycetes.*	
Chytridiales.	*Rhizophidium, Synchytrium.*
Saprolegniales.	*Saprolegnia.*
Monoblepharidales.	*Monoblepharis.*
Peronosporales.	*Pythium, Peronospora, Cystopus.*
Mucorales.	*Mucor.*
(iii) *Ascomycetes.*	
Plectascales.	*Aspergillus.*
Erysiphales.	*Sphaerotheca, Erysiphe.*
Pezizales.	*Pyronema, Peziza.*
Helvellales.	*Helvella.*
Phacidiales.	*Rhytisma.*
Saccharomycetales.	*Saccharomyces, Schizosaccharomyces.*
Hypocreales.	*Claviceps.*
Sphaeriales.	*Hypoxylon.*
Laboulbeniales.	*Stigmatomyces.*
(iv) *Basidiomycetes.*	
Urediniales.	*Puccinia.*
Ustilaginales.	*Ustilago.*
Aphyllophorales.	*Polyporus.*
Agaricales.	*Psalliota.*
Gasteromycetales.	*Cyathus, Phallus.*

C. BACTERIA.

Eubacteriales.

D. LICHENES.

Ascolichenes.	*Peltigera.*

CHAROPHYTA

Charales.	*Chara.*

BRYOPHYTA

A. HEPATICAE.

Jungermanniales.	*Pellia.*
Marchantiales.	*Marchantia.*
Anthocerotales.	*Anthoceros.*

B. MUSCI.

Bryales.	*Mnium, Polytrichum.*
Sphagnales.	*Sphagnum.*

PTERIDOPHYTA *

A. PSILOPSIDA.

Psilotales.	*Psilotum.*

B. LYCOPSIDA.

Lycopodiales.	*Lycopodium, Selaginella.*
Isoetales.	*Isoetes.*

C. SPHENOPSIDA.

Equisetales.	*Equisetum.*

D. PTEROPSIDA.

Filicales.	*Botrychium, Marattia, Osmunda, Hymenophyllum, Dryopteris, Pteridium, Azolla.*

SPERMATOPHYTA *

A. GYMNOSPERMAE.

Cycadales.	*Cycas.*
Ginkgoales.	*Ginkgo.*
Coniferales.	*Pinus.*
Taxales.	*Taxus.*
Gnetales.	*Ephedra, Gnetum, Welwitschia.*

B. ANGIOSPERMAE.

- (i) *Dicotyledons.*
    - Archichlamydeae.
    - Metachlamydeae.
- (ii) *Monocotyledons.*

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* Fossil groups are not included in this classification (see note on p. 46).

CHAPTER IV

THE ALGAE : EUGLENOPHYCEAE, CHLOROPHYCEAE AND CYANOPHYCEAE

THE Phylum **Thallophyta** includes all those lowly plants which are devoid of stem, root and leaves. In the Algae and Fungi the simpler forms consist of a single cell or of a small colony of cells, while in the higher forms the body, or **thallus,** consists either of a **filament** of cells joined end to end, or, in the more complex types, of cellular tissue or of a system of filaments, some running longitudinally and some transversely, the whole being embedded in **mucilage.** The method of nutrition is holophytic. Chlorophyll is present only in the Algae, and here its presence may be masked by other pigments. Sexual reproduction occurs in most Thallophytes, but the process varies enormously and shows very instructive stages of evolutionary development towards increased complexity in the Algae and towards simplification and reduction in the Fungi. Sexual reproduction is unknown in Euglenophyceae.

The Bacteria are usually included in this phylum. They are either unicellular or filamentous, they are devoid of chlorophyll, and reproduction is by a simple process of fission.

The phylum Thallophyta is subdivided into the following groups :—

1. **Algae** (*e.g.*, Seaweeds).
2. **Fungi** (*e.g.*, Moulds, Mushrooms and Toadstools).
3. **Bacteria.**
4. **Lichenes.**

ALGAE

The Algae are aquatic or semi-aquatic Thallophyta in which all or most of the cells of the thallus normally contain chlorophyll. The simpler types are unicellular, but in the higher forms the thallus may become complicated and of large size, with a considerable amount of cellular differentiation. Except in the Euglenophyceae reproduction is both sexual and asexual. In the simpler members sexual reproduction consists of the fusion in pairs of exactly similar, motile cells, called **isogametes,** while in the higher types distinct sex organs are developed, which consist of **antheridia,** the male organs, and **oogonia,** the female organs. The different gametes produced in these sex organs may be shed and fuse externally (**heterogamy**), or the female may be retained within the body of the plant and be fertilized by a motile male gamete (**oogamy**).

The Algae are classified according to the colour of the pigment present in the cells. The following are the more important groups :—

1. **Euglenophyceae** (Motile organisms, devoid of a cell wall, either colourless or containing chlorophyll, often with various additional pigments.

2. **Chlorophyceae** (Green Algae, containing chlorophyll only).
3. **Cyanophyceae** (Blue-green Algae, containing phycocyanin in addition to chlorophyll).
4. **Phaeophyceae** (Brown Algae, containing fucoxanthin in addition to chlorophyll).
5. **Bacillariophyceae** (Diatoms, containing diatomin in addition to chlorophyll).
6. **Rhodophyceae** (Red Algae, containing phycoerythrin and phycocyanin in addition to chlorophyll).

EUGLENOPHYCEAE

The Euglenophyceae include both green and colourless organisms. Those which possess chlorophyll are able to assimilate carbon dioxide and live as plants. Those which are colourless may either live as saprophytes, or holozoically like animals by ingesting solid food. The Euglenophyceae were formerly included in the old group known as the **Flagellata** which it was impossible to classify collectively either as plants or animals ; but according to recent methods of classification the Flagellata are split up into a number of separate groups, some of which are placed in the Thallophyta, among the Algae, while others form a separate group of the Protozoa among the animals. In the past it was not uncommon to consider the whole group of the Flagellata as members of the Protozoa, green and colourless alike, and moreover to extend the scope of the group to include many unicellular and colonial Chlorophyceae, a system which still survives in some quarters, though certainly erroneous.

In the Euglenophyceae there is no definite cell wall, merely a denser protoplasmic surface layer, with the result that the protoplast may exhibit contractile and amoeboid movements. One or more mobile appendages, the **flagella,** are present, and the motile condition is dominant in the life history. **Pulsating vacuoles** are present. The organisms may live independently or may unite to form colonies held together by mucilage or possessing stalked investments.

Sexual reproduction is unknown. Multiplication is by **binary fission** as the result of a longitudinal split of the protoplast during the motile phase. Many produce thick-walled resting spores. The Euglenophyceae contain the single order Euglenales. We shall consider one common green example of the group, *Euglena viridis.*

Euglena viridis

This little organism is found very commonly in fresh-water ponds and ditches, where it may at times occur in vast numbers producing a green colouration of the whole of the water. There are, however, a number of allied species, some of which occur in brackish or even in sea water.

The organism (Fig. 28) consists of a single oval or fusiform protoplast which often terminates in a point at the posterior end and is enclosed in a spirally striated membrane. The upper or anterior end of the organism is rounded, and slightly to one side is an indentation into the protoplast, leading to a canal through which passes out a single flagellum about as long as the body of the organism. At the base of this canal lies a large vacuolar reservoir which has a thickening at its upper end which may act as a sphincter for opening and closing the canal. Near the reservoir are one or more pulsating vacuoles which may fuse with, or in any case discharge their contents into, the reservoir. Adjacent to the reservoir is a prominent red **eye spot** which has been shown to be light-sensitive.

The nucleus (Fig. 29) occupies a posterior position. It is surrounded by a colourless area of cytoplasm. The chlorophyll is contained in a series of about ten rod-like chloroplasts which radiate out from the centre of the cell. Each chloroplast has, at the end nearest the centre, a group of large solid granules of **paramylon** of very diverse shapes. These grains actually develop in the cytoplasm but come to lie attached to the inner ends of the chloroplasts. Paramylon is a polysaccharide allied to starch. It differs, however, in giving no colour with iodine, and it is not attacked by the enzyme diastase.

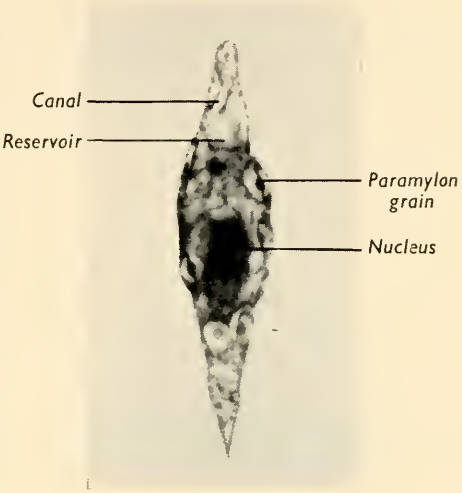


FIG. 28.—*Euglena viridis.* Stained preparation showing nucleus and paramylon grains.

A few species of *Euglena* are devoid of chlorophyll. Some live as saprophytes, even in the intestines of animals, such as frogs and tadpoles, while a few have been described as capable of ingesting solid food material.

The organisms are all capable of active movement, swimming by the lashing of the flagellum and the corkscrew-like turning of the whole body. They also perform a characteristic, rhythmical and contractile motion, termed **euglenoid** movement. The flagella show an axial thread with a protoplasmic sheath, and there are indications that the axial thread itself consists of a spiral strand of still finer fibres.

REPRODUCTION

Reproduction is effected by the longitudinal division of the body into two. This is called **binary fission**. In most instances the individual comes to rest, secretes an envelope of mucilage, and then proceeds to divide, beginning at the front end of the protoplast. In some species the cells so formed may round themselves off and divide again and again, so that a large number of spherical cells are formed all enclosed in the original membrane. Eventually this breaks and the individuals separate and grow into normal euglenoid

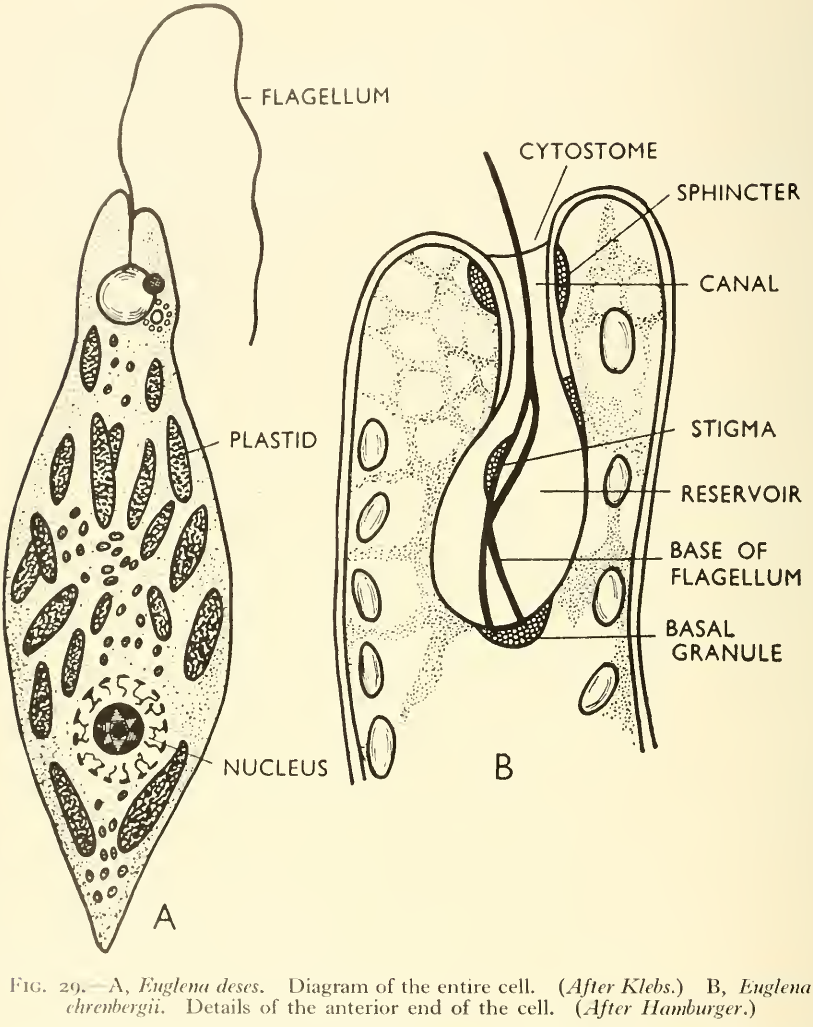


FIG. 29.—A, *Euglena deses.* Diagram of the entire cell. (*After Klebs.*) B, *Euglena ehrenbergii.* Details of the anterior end of the cell. (*After Hamburger.*)

cells. In dividing while at rest *Euglena* differs from the majority of the other Flagellates, and shows an approach to the true Algæ.

Cysts with thick walls are frequently found ; they are generally spherical and the walls are striated. Very often such cysts are red in colour due to a red pigment, **haematochrome,** in the cells. Such encystment may be only temporary, and the individual may retain its flagellum. If, however, the process is employed to tide the organism over a longer period of unfavourable conditions the enclosed cell may retract its flagellum.

Except in one doubtful case sexual reproduction is unknown in any species of *Euglena.*

CHLOROPHYCEAE

The Chlorophyceae are Algae in which the only pigment is chlorophyll. It is contained in special bodies within the cells, which are termed **chloroplasts.** The shape and arrangement of these chloroplasts varies greatly in the different groups, and is frequently used as a means of classification. Among higher plants the chloroplasts are remarkably uniform in shape, but it is evident that the Green Algae are still in an experimental stage of evolution in this respect and that fixity of form has not been attained.

The lower members are unicellular or colonial. The higher members are mostly filamentous, but a few form flat thalli consisting of cells which divide in two planes. In certain types the body of the organism consists of a single giant cell containing many nuclei ; such a structure is termed a **coenocyte.** Occasionally the thallus may be made up of a number of coenocytes embedded in mucilage.

The Green Algae occur mostly in fresh water, though a few are found in the sea, and some occur on land, but generally in moist situations. In fact quite a large number have been isolated from the soil, though all of very simple types.

The method of reproduction varies considerably. In some species both sexual and asexual reproduction occurs, the former either by isogametes or by complex antheridia and oogonia ; the latter by small motile bodies termed **zoospores.** This name recalls the belief of early naturalists that in producing these motile cells the plant was actually turning into an animal.

The Chlorophyceae are divided into a number of Orders, of which we shall consider types from the following :—

1. **Volvocales** (*e.g.*, *Chlamydomonas*, *Haematococcus*, *Gonium*, *Pandorina*, *Eudorina*, *Volvox*).
2. **Chaetophorales** (*e.g.*, *Pleurococcus*, *Coleochaete*).
3. **Ulotrichales** (*e.g.*, *Ulothrix*).
4. **Oedogoniales** (*e.g.*, *Oedogonium*).
5. **Conjugales** (*e.g.*, *Spirogyra*).
6. **Siphonales** (*e.g.*, *Bryopsis*, *Vaucheria*).
7. **Siphonocladiales** (*e.g.*, *Cladophora*).

Volvocales

The Volvocales are Chlorophyceae in which the thallus is unicellular or colonial, and is generally motile throughout life. In the colonial forms separate cells may be embedded in a common envelope of mucilage, and the cells may be systematically linked together by fine protoplasmic threads. The vegetative cells possess extremely fine thread-like **flagella,** which project through the wall of the cell and are capable of active motion. In the Volvocales each cell is generally provided with a pair of flagella of equal length, attached to the anterior end of the cell. They are frequently retracted or shed during periods of rest. Asexual reproduction takes place by the formation of zoospores. Most genera also reproduce sexually, and the simpler members are isogamous. The cell is generally bounded by a cell wall, which may either be delicate or firm and rigid. In the latter case it consists of cellulose. There is usually a single chloroplast situated at the posterior end of the cell and containing a single **pyrenoid**, or starch-forming centre. There is a central nucleus and one, or more commonly two, **contractile vacuoles,** which show a rhythmical alternation of rapid contraction (systole) and slow expansion (diastole). They are apparently excretory organs, and in certain forms are known to contain uric acid.

We shall consider in detail the following members of this group: *Chlamydomonas*, *Haematococcus*, *Gonium*, *Pandorina*, *Eudorina*, *Volvox*.

Chlamydomonas

This organism is very common in fresh waters, sometimes forming a green scum over the surface, and sometimes colouring whole ponds a turbid green. The vegetative cell (Fig. 30) is usually oval and is enclosed in a cellulose wall with the protoplast closely applied to it. The cellulose wall distinguishes *Chlamydomonas* from *Euglena*. The chloroplast is basin-shaped, with its base at the hinder end of the cell, the nucleus being situated in the centre. There is a single **pyrenoid** in the lower part of the chloroplast, which acts as a centre around which starch is formed. The pyrenoid itself stains brown with iodine and is usually more conspicuous than the nucleus.

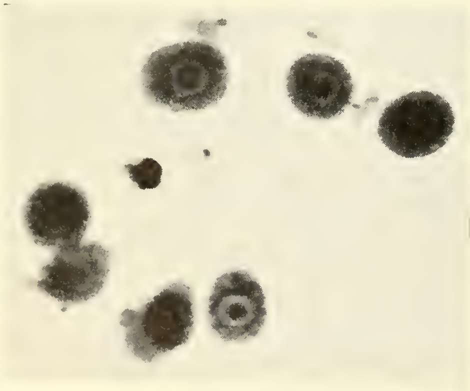


FIG. 30.—*Chlamydomonas*. Photograph showing the appearance of the vegetative cells. The prominent central granule is the nucleus. The flagella are not stained and do not show.

At the anterior end of the cell two long **flagella** (Fig. 31) pass out through the cell wall, each arising from a **basal granule,** and between them the cell wall is often slightly protruded in the form of a **beak.** Close to where the flagella arise two **contractile vacuoles** are formed.

When food and oxygen are plentiful the organism swims actively about by means of its flagella which, by their rapid circular motion, act as tractor propellers, drawing the organism along at a good speed, flagella foremost, with a spiral movement.

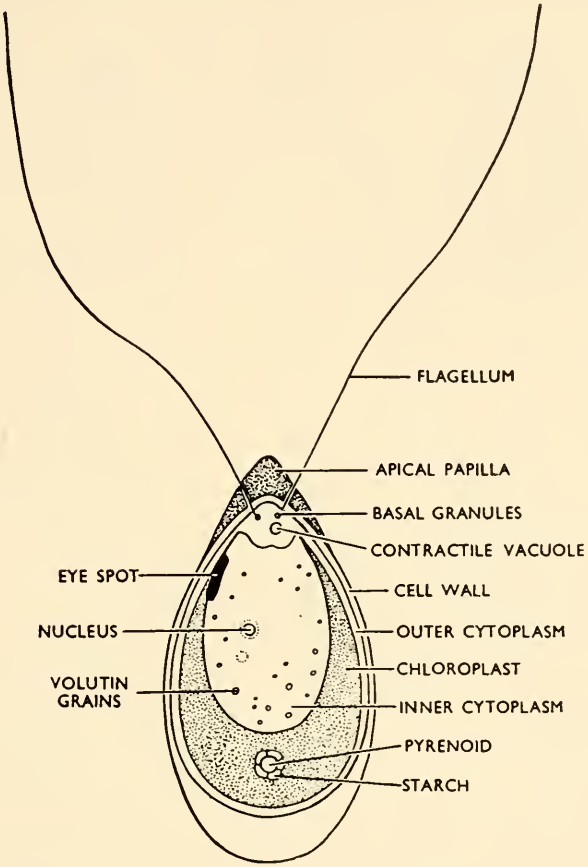


Fig. 31.—*Chlamydomonas*. Diagram showing the complete structure of the vegetative cell. (*After Pascher*.)

The water and inorganic salts required for life are absorbed over the whole surface of the cell. The water contains dissolved carbon dioxide which, in the presence of light and chlorophyll, is combined with water to form sugar and starch. The starch is formed as little grains, clustered round the pyrenoid. The cell is attracted towards light of moderate intensity, the response being apparently due to the sensitiveness to light of a tiny spot of red carotinoid pigment at the forward edge of the chloroplast. This **eye spot** or **stigma** is covered by a minute lens in the thickness of the cell wall and is supposed to function as an extremely primitive eye.

REPRODUCTION

Reproduction may be sexual or asexual (Fig. 32). In asexual reproduction the active cell comes to rest, the flagella are withdrawn, and the contents of the cell divide up into four, eight or sixteen parts, which become **zoospores**. A zoospore is a motile cell, very similar to the parent cell but smaller. It may either become active and swim away or may remain enclosed by the parent wall and grow and divide again, so that under some conditions a large number of zoospores, usually without flagella, may be found clustered together inside an envelope of mucilage. This aggregation of cells is spoken of as the **palmella** stage, from its resemblance to another Alga of that name. The cells easily revert, however, to the motile condition (Fig. 33).

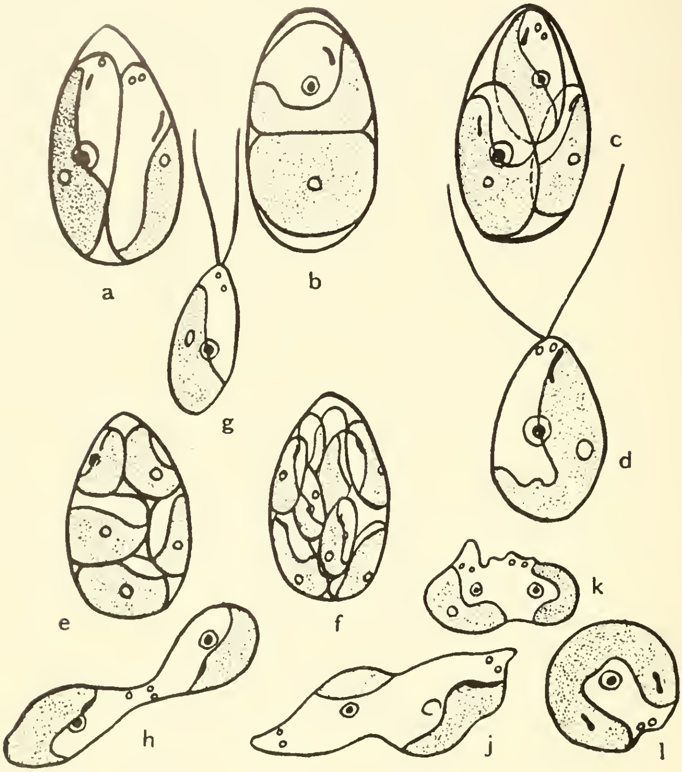


FIG. 32.—*Chlamydomonas*. Stages in reproduction. A to C, Stages in the division of the cell into zoospores. D, Mature zoospore. E and F, Stages in the division of the cell into gametes. G, Mature gamete. H to L, Stages in the fusion of the gametes. (*After Pascher*.)

FIG. 33.—*Chlamydomonas*. Cell in asexual reproduction, Palmella stage.

In sexual reproduction the active cell comes to rest and the flagella are withdrawn. The contents then divide up into either thirty-two or sixty-four **gametes.** These also resemble the parent cells, except that they are much smaller and are devoid of a cell wall. Under suitable conditions they are liberated by the bursting of the parent cell. They then fuse in pairs, each pair forming a **zygote**. In fusion the two anterior ends come together and the contents of the one gamete pass into the other. The zygote then secretes a thick wall and thus becomes a **cyst**. There is usually no difference in the size or structure of the gametes, and hence they are said to be **isogamous.** In some species, however, the gametes are alike in structure but differ in size, and they are then termed **heterogamous** or **anisogamous.**

In *Chlamydomonas braunii* the gametes are dissimilar in size. **Macrogametes** are produced in fours from the parent cell, which they resemble ; while the **microgametes,** which are formed in eights, are only about half the size and more elongated. The macrogamete soon comes to rest, withdraws its flagella and is sought after by the active microgamete. Both possess a cell wall, and after union by their apical ends the membranes coalesce and the contents of the microgamete pass over into the macrogamete. During this process the flagella disappear and a close-fitting membrane is secreted by the zygote. In this species, therefore, *Chlamydomonas* approaches an oogamous condition.

The life-history of *Chlamydomonas* may be represented in the form of a diagram (Fig. 34) showing the succession of stages which occur both in sexual and asexual reproduction.

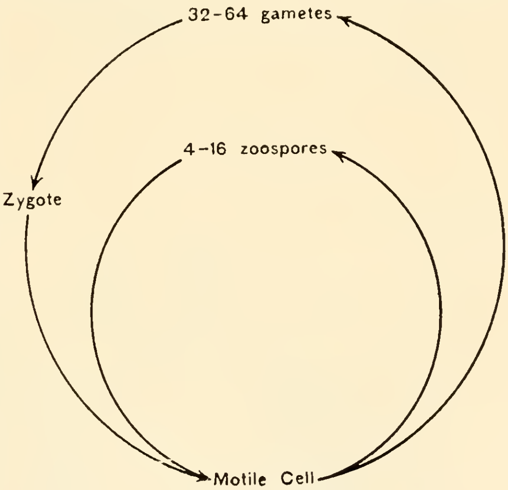


FIG. 34.—Life-cycle of *Chlamydomonas.*

Haematococcus (Sphaerella)

The active cell in this organism differs from that of *Chlamydomonas* (Fig. 35) chiefly in the separation of the protoplast from the cell wall. The cell wall itself is well defined but thin and is composed of cellulose. It is separated from the cytoplasm by a thick mucilaginous inner wall which is penetrated by fine protoplasmic threads. Embedded in the central cytoplasm is a large hemispherical chloroplast which is hollowed out and resembles that in *Chlamydomonas.* In fact the structure of the whole protoplast is substantially similar to that of *Chlamydomonas,* except that there are numerous contractile vacuoles and several pyrenoids.

Haematococcus obtains its name from the fact that the cell is often red in colour. This is due to the presence of a carotinoid red pigment, **haematochrome,** which masks the green colour of the chlorophyll. The actual colour of any particular cell depends upon the relative proportion of haematochrome present, which in turn depends on the supply of nitrogen compounds. The Alga very readily forms **cysts** by the withdrawal of the flagella and the rounding up of the cell, in fact it is in this condition that the organism is generally seen.

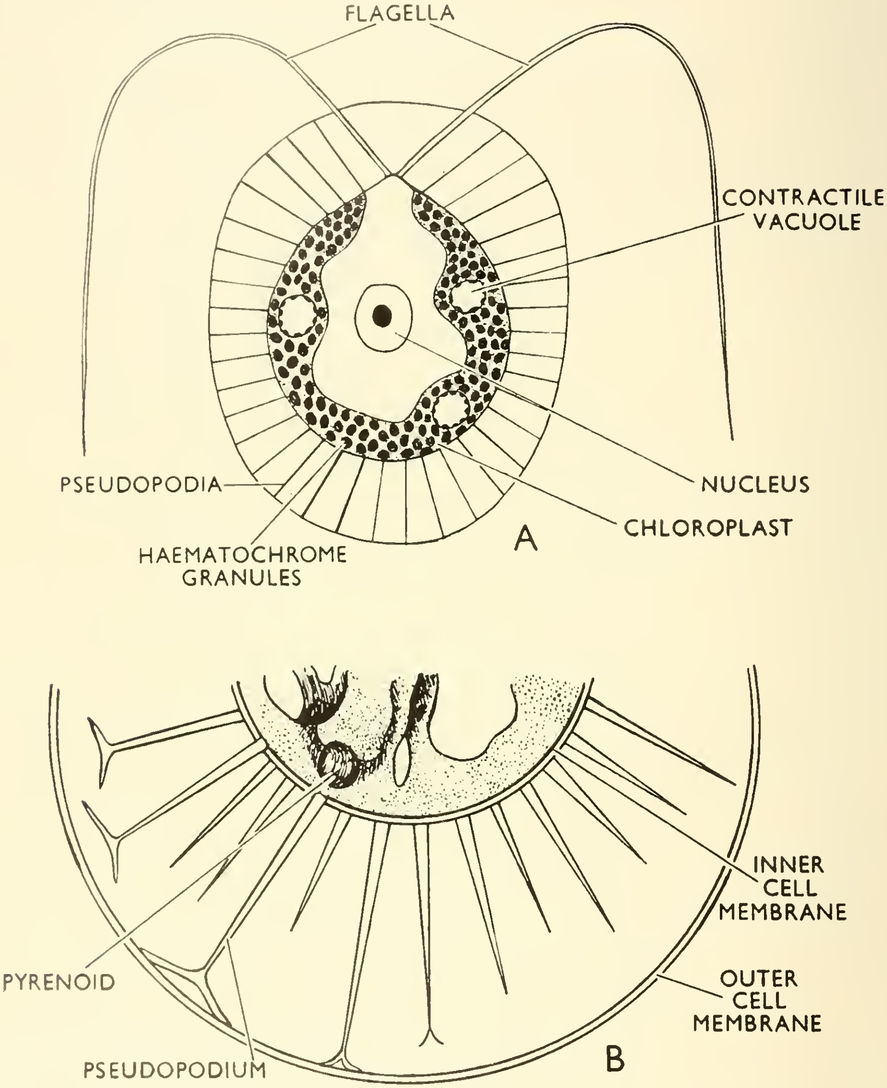


Fig. 35.—*Haematococcus pluvialis.* A, Diagram showing the complete structure of the vegetative cell. B, Posterior portion of a cell, enlarged to show the details of the wall structure. (*After Pascher.*)

Haematococcus nivalis is closely similar to the type we have described. The resting cells contain an abundance of red pigment and, since the Alga is found on the snow in Alpine and Arctic regions, it gives the appearance of blood-red patches, from which it has gained the name of the " red-snow " plant. It also sometimes comes down in great quantities in rain, thus giving rise to stories about " rains of blood."

REPRODUCTION

Reproduction is usually carried out by simple longitudinal division of the motile cell, no zoospores being formed. The contents of a cyst may sometimes divide to form an extensive **palmella stage,** and it is from such resting cells that the gametes are formed. They are minute motile swarmers, with no cell wall, but otherwise like the normal cell.

Turning now from the unicellular types to the colonial ones, we find various examples consisting of a number of chlamydomonas-like cells embedded in mucilage. The size of these colonies varies according to the number of cells concerned. Both in shape and in the number of component cells each species is quite distinct and constant. We shall consider here four examples, *Gonium*, *Pandorina*, *Eudorina* and *Volvox*.

Gonium

This is the simplest of the colonial Volvocales. The colony or **coenobium** consists of a sixteen-celled plate (Fig. 36), which is square in surface view but thin and slightly curved in side view. It is made up of four central and twelve peripheral cells, each having the chlamydomonad structure. The cells are connected by slight protrusions so that triangular spaces are formed between them, while the centre is made up of a squarish area of mucus. The

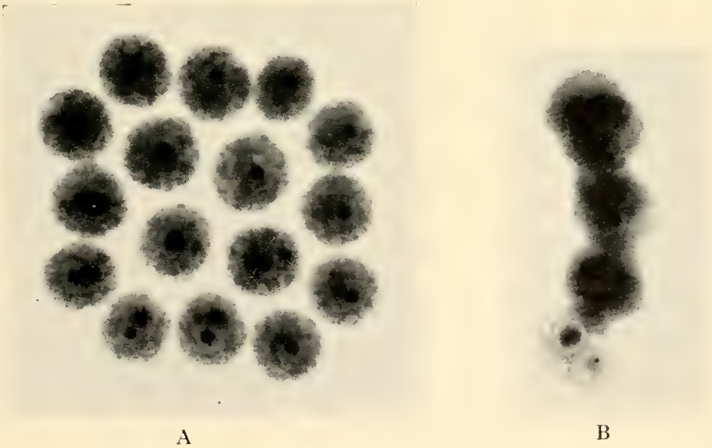


FIG. 36.—*Gonium sp.* A, Surface view of a mature colony. B, Colony in side view showing the curvature.

whole coenobium is embedded in mucilage which possesses a firm boundary layer. The peripheral cells are inclined at an angle to the vertical axis of the plate, and each possesses a pair of long equal flagella which are directed towards the convex surface. When in motion the whole plate spins round on its axis and moves with the convex surface forwards.

Reproduction

Gonium reproduces both asexually and sexually (Figs. 37 and 38).

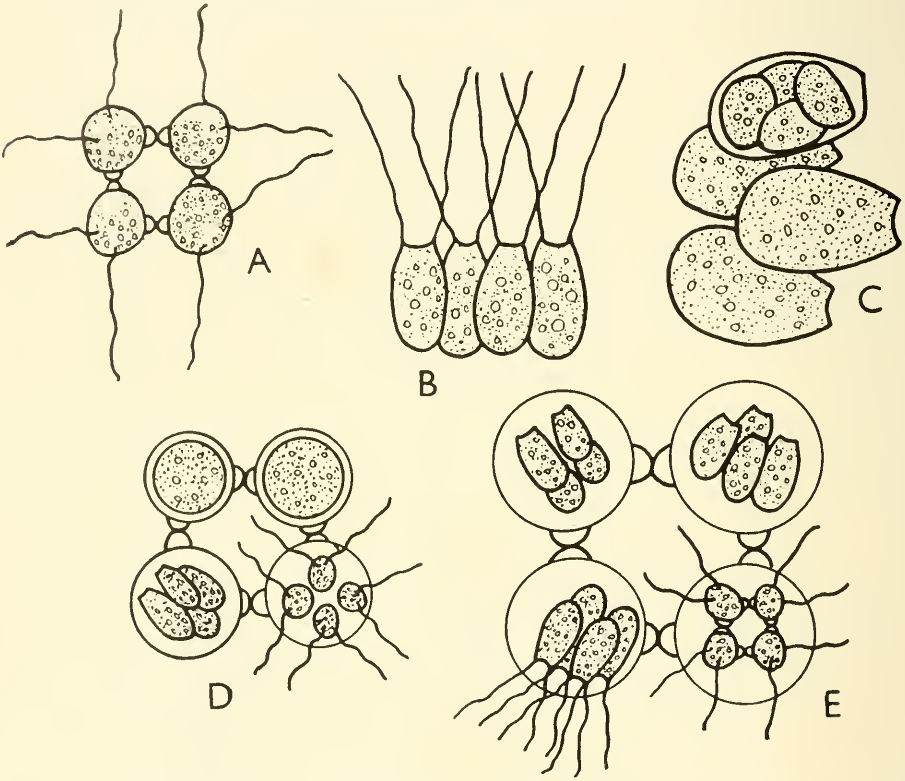


Fig. 37.—*Gonium lacustre.* Stages in asexual reproduction. A, Four-celled colony. B, The same in side view. C, Beginning of sub-division of the cells of the colony. D, Cell division more advanced, one group of daughter cells already flagellated. E, Sub-division of cells complete. Two daughter colonies ready for liberation. (*After West.*)

In asexual reproduction all the sixteen cells of the colony divide simultaneously, each forming a daughter colony of sixteen cells. The divisions of each cell are all longitudinal. If a cell of a *Gonium* colony be artificially detached it at once divides up so as to form a new colony of normal size.

Sexual reproduction is by means of naked **isogametes** which are produced in sexual coenobia of small size. The gametes are liberated from the coenobium by the breakdown of the surrounding membrane. Gametes from the same colony do not fuse together, in fact there appears to be a physiological difference between these sexual coenobia although they all look alike.

Gametes from one type of coenobium fuse only with those of another. The zygote so formed is at first quadriflagellate, it comes to rest and rounds off. A membrane is formed and a prolonged period of rest may follow. On germination the zygote divides to produce four cells which form a plate, and from each of these a fresh sixteen-celled coenobium is produced. It is probable that the reduction division occurs during the first two divisions of the zygote, for it has been shown that there is a sexual segregation at this stage whereby two of the daughter coenobia are sexually distinct from the other two.

FIG. 38.—*Gonium sp.* Colony in process of asexual reproduction. Daughter colonies in various stages of development, one being already completed.

Pandorina

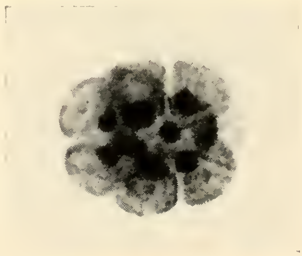


FIG. 39.—*Pandorina morum.* Stained preparation of a colony showing the cell nuclei.

The colony consists of sixteen cells, each like a single *Chlamydomonas* cell (Fig. 39). The cells are rather pyramidal in shape and are arranged in an oval group with their pointed ends inwards. They are closely packed together, and the whole coenobium is surrounded by a mucous investment. Each individual cell has two widely divergent flagella, by means of which the whole colony is propelled along, generally with a definite anterior end, in the cells of which the eye-spots are larger and better developed.

REPRODUCTION

Reproduction is both sexual and asexual (Fig. 40). Asexual reproduction consists in the formation of daughter colonies within the cells of the parent.

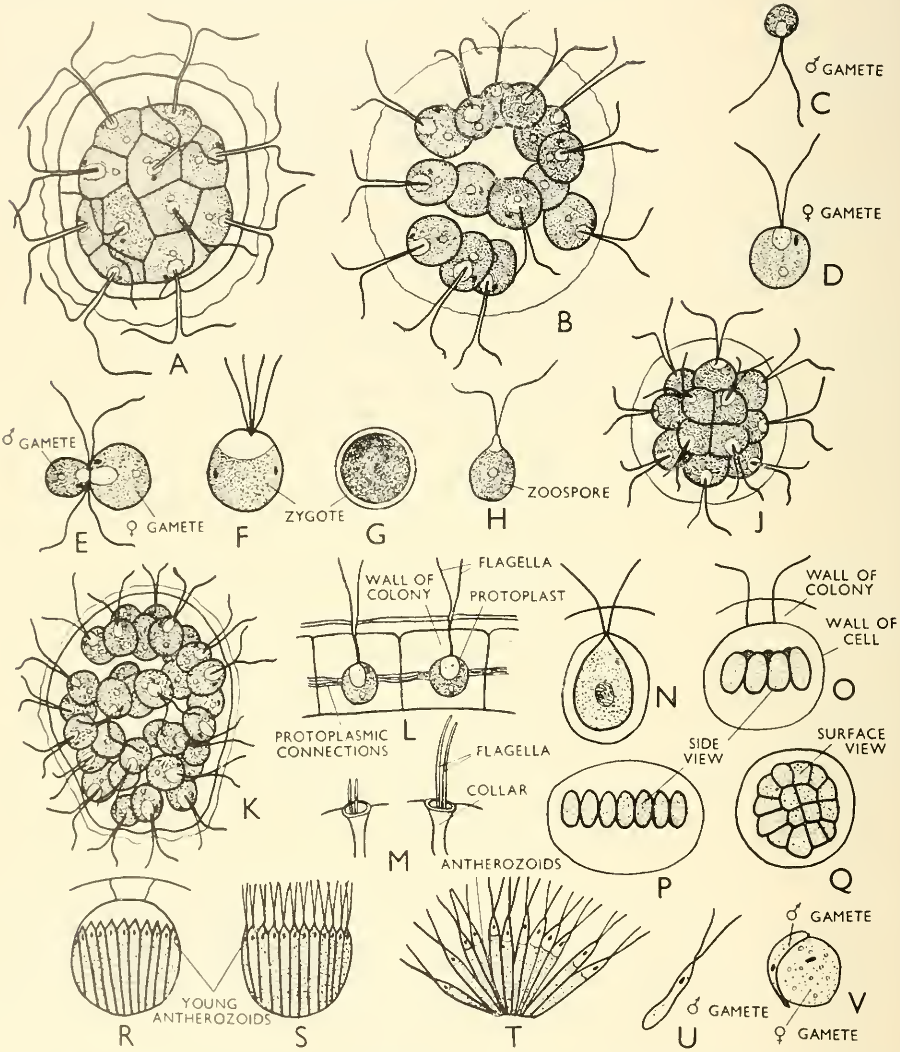


FIG. 40.—*Pandorina.* Stages in reproduction. A, Mature colony. B, Colony of female gametes. C, Male gamete. D, Female gamete. E, Conjugation. F, Zygote. G, Resting zygote. H, Zoospore. J, Young colony formed from zoospore.

Eudorina. Stages in reproduction. K, Mature colony. L, Detail of vegetative cells. M, Detail of the emergence of flagella through the wall of the colony. N, Cell destined to form antheridium. O to T, Stages in the formation of antherozoids. U, Antherozoid. V, Conjugation of gametes. (*After Fritsch.*)

Each cell divides into sixteen cells, which at first form a curved plate. This later becomes flat and then curves in the reverse direction, the corners meeting to form a hollow coenobium. This is liberated as a new colony after the breakdown of the parent cell. This inversion of the daughter colonies during development should be compared with that described in *Eudorina* and *Volvox*. The liberation of independent zoospores rarely occurs.

Sexual reproduction consists in the liberation of the naked protoplasts of the cells, which escape from the membranes and become the gametes. Conjugation is usually isogamous, but there is a tendency towards a preferential fusion of gametes of unequal size, thus showing an advance towards anisogamy, which becomes much more pronounced in *Eudorina* and *Volvox*.

The zygote germinates to liberate a single zoospore, which divides to form a new colony. Four cells are actually formed by the germinating zygote, but only one of these survives to form a zoospore, while the other three abort. This suggests that meiosis probably occurs at this stage, as in *Gonium*.

Eudorina

In *Eudorina* the colony is larger than in *Pandorina*. It is oval in shape and consists generally of thirty-two globose cells, loosely arranged on the periphery of a hollow mucilaginous matrix (Fig. 41). The biflagellate cells are of the typical chlamydomonad type, but the chloroplast often has several pyrenoids and the cells show a progressive reduction in the size of the eye-spot as we pass from the anterior to the posterior end of the colony. Unlike *Pandorina*, the cells forming the colony are connected together by extremely fine protoplasmic strands, only visible after special staining. The flagella are long and pass outwards from the cells through minute open funnels in the mucilage investment (Fig. 40, M).

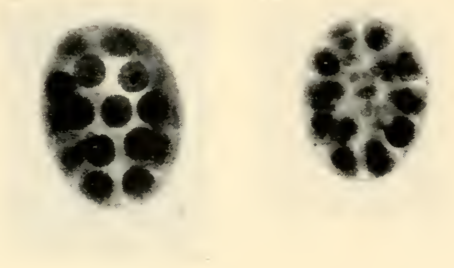


FIG. 41.—*Eudorina*. Colony in surface view and in optical section.

REPRODUCTION

Asexual reproduction (Fig. 42) consists in the formation of daughter colonies within the individual parent cells, whose protoplasts divide up into a number of parts equal to the number of the cells of the new colony (Fig. 43). The young colony is at first flat, but finally curls over to form a hollow sphere. This new colony is liberated by the breakdown of the parent cell wall. As all the cells reproduce simultaneously in this way the parent colony naturally disappears after reproduction.

Sexual reproduction is more complex than in *Pandorina* and shows a definite advance, to **oogamy,** the gametes being quite distinct in appearance and behaviour. The colonies are generally **dioecious,** that is to say, the male and female gametes are formed in different colonies. In the female colony the cells enlarge somewhat and become the female gametes, or **oospheres,** which, when mature, are fertilized *in situ*. In male colonies the cells divide to form groups of sixty-four **antherozoids,** yellowish in colour, and each with two flagella. These are liberated as groups which swim to the female colonies, where the antherozoids separate. The zygotes germinate as in *Pandorina*.

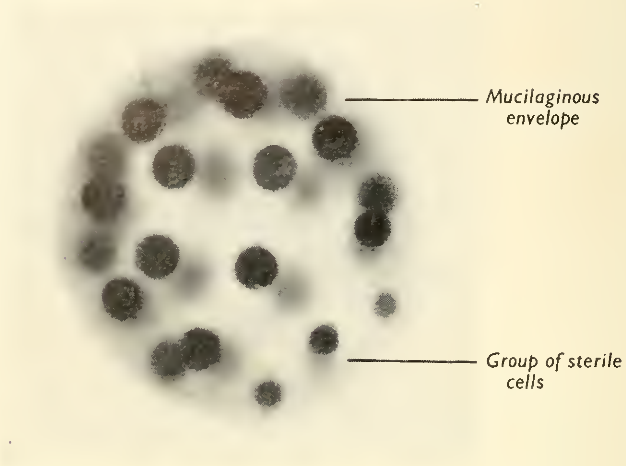


FIG. 42.—*Eudorina illinoisensis.* Vegetative colony showing the four small cells at the posterior end which do not reproduce.

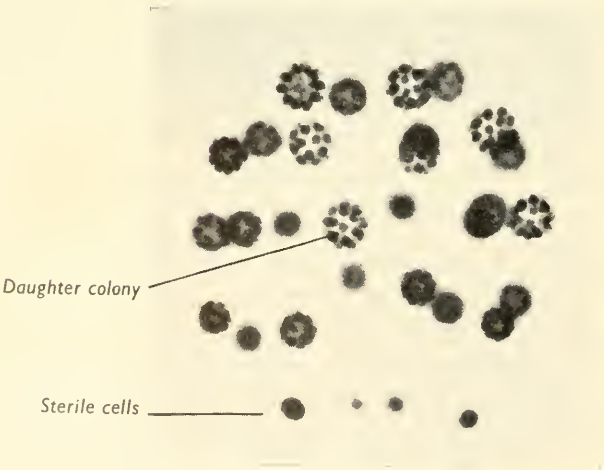


FIG. 43.—*Eudorina illinoisensis.* Reproduction colony showing daughter colonies forming in all cells except the four posterior cells.

Volvox

In *Volvox* we have the largest colony of this type which is known (Fig. 44). It consists of a hollow sphere or ellipsoid of up to 20,000 cells, forming a peripheral layer within the mucous sheath (Fig. 45). The individual cells are of the general chlamydomonad type, with globose, oval or stellate chloroplasts, often with several contractile vacuoles and one or more pyrenoids. The cell walls are thick and gelatinous, often with a firmer middle lamella which forms a polygonal pattern between the cells. The cells of the colony are connected together by means of protoplasmic strands. These may be very slender, but in *Volvox globator* they are thick processes

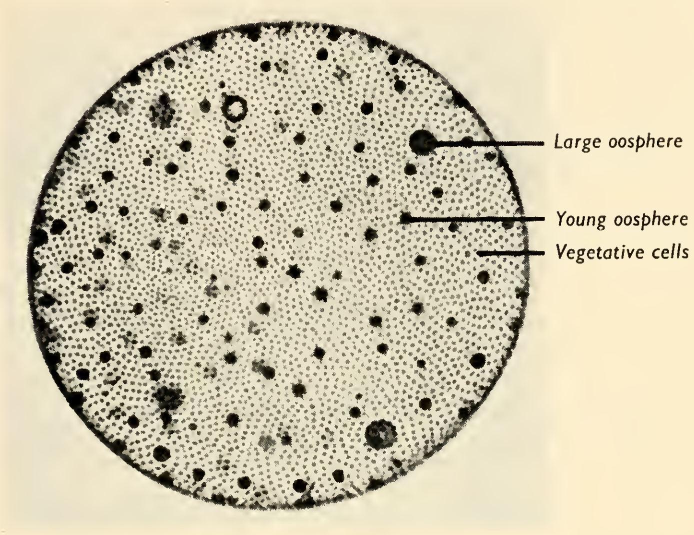
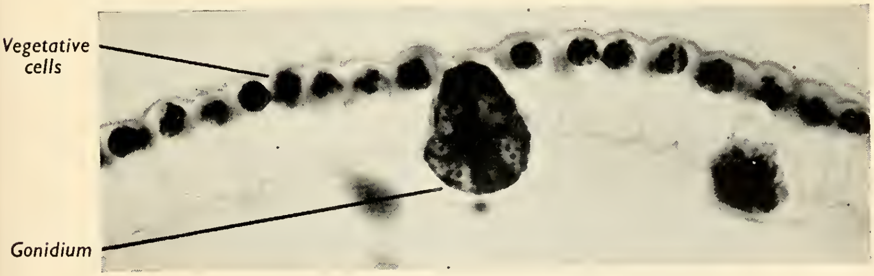


FIG. 44.—*Volvox aureus.* Entire mature colony in surface view showing vegetative and reproductive cells.



[*By courtesy of the Biological Supply House Inc., Chicago, U.S.A.*

FIG. 45.—*Volvox aureus.* Detail of the colony surface in transverse section showing the layer of vegetative cells and an enlarging gonidium.

which are linked together by fine strands passing through the middle lamellae (Fig. 46). Each cell is thus very similar to *Haematococcus*. The whole colony moves and rotates slowly by the concerted action of the flagella, two of which project through the mucus from the anterior end of each cell.

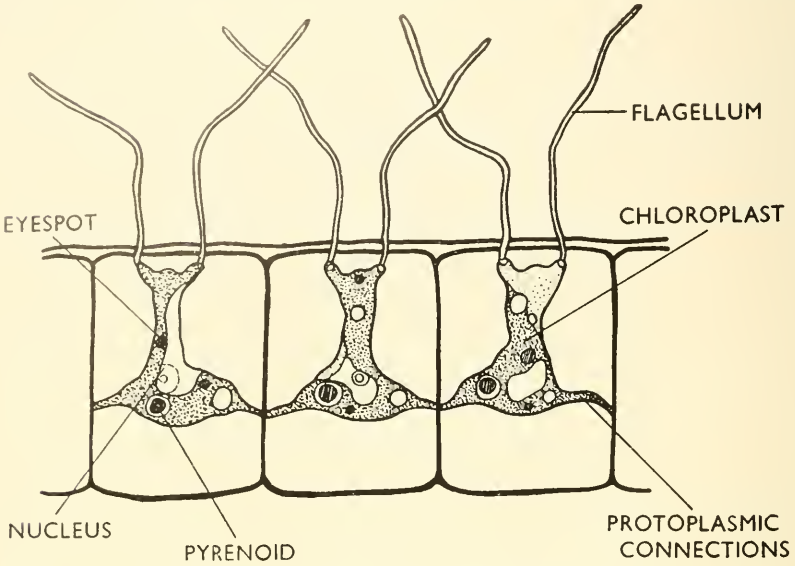


Fig. 46.—*Volvox rousseletii*. Details of the structure of the vegetative cells which form the periphery of the colony. (*After Rich.*)

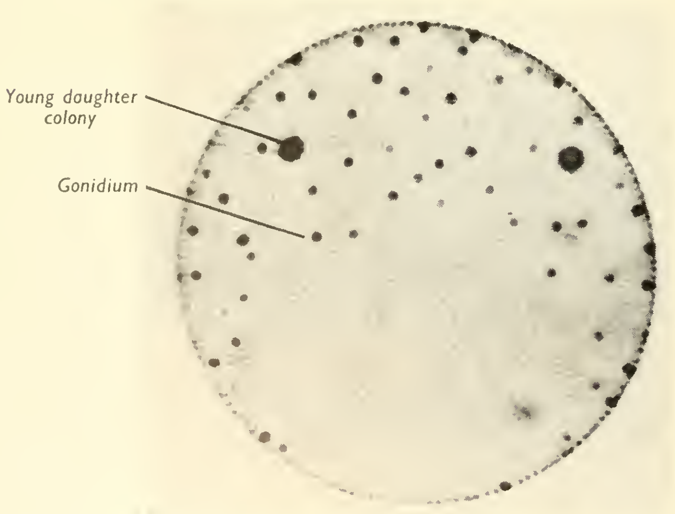


Fig. 47.—*Volvox aureus*. Entire colony seen in optical section showing the peripheral layer of vegetative cells and a number of enlarging gonidia.

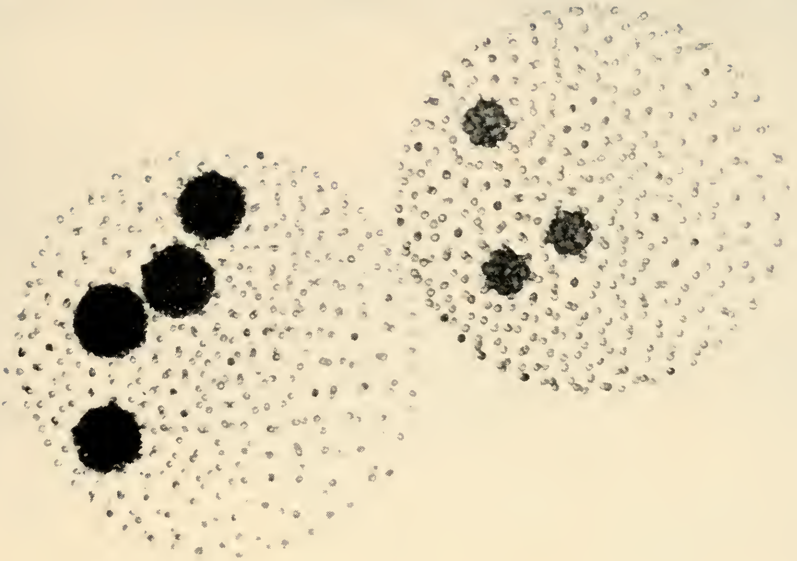


FIG. 48.—*Volvox aureus.* Two colonies showing early stages in the development of daughter colonies from gonidia.

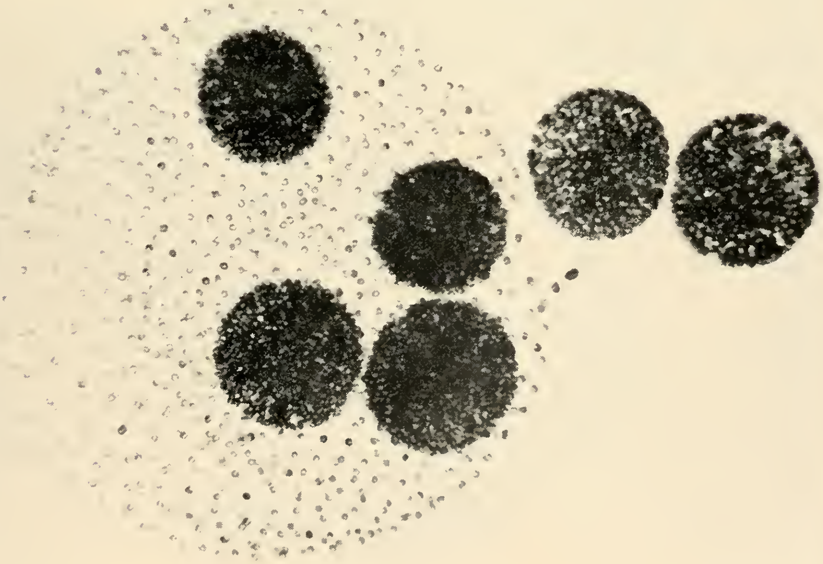


FIG. 49.—*Volvox aureus.* Colony with mature daughter colonies in process of liberation.

Reproduction

Asexual reproduction takes place by the formation of daughter colonies within special cells of the parent colony, which are recognizable by their greatly increased size and are called **gonidia** (Fig. 47). By repeated cell divisions the gonidia produce hollow, spherical colonies, which project into

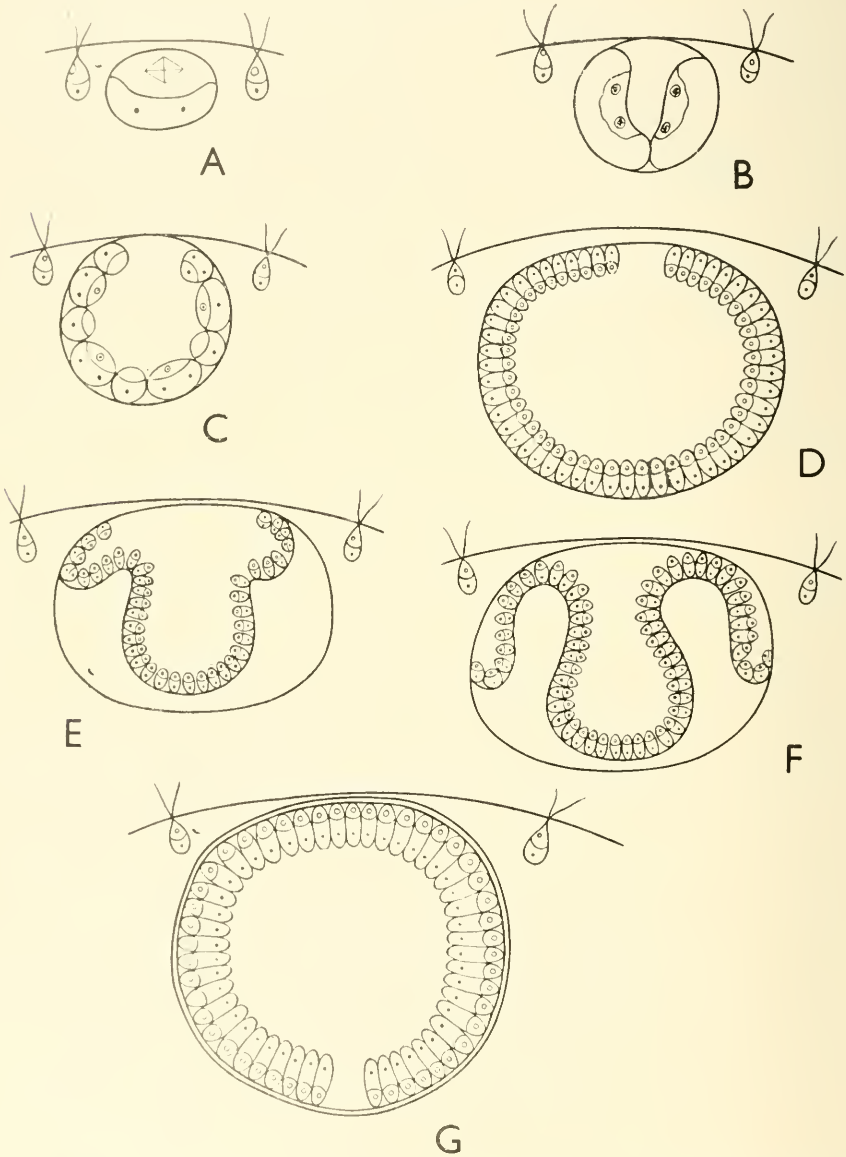


Fig. 50.—*Volvox aureus.* Diagram showing stages in the development of an asexual daughter colony. A, Gonidium in the peripheral layer. B, C and D, Stages in the building up of the daughter colony by division of the gonidium. E and F, Stages in eversion. G, Mature daughter colony fully everted. (*After Zimmermann.*)

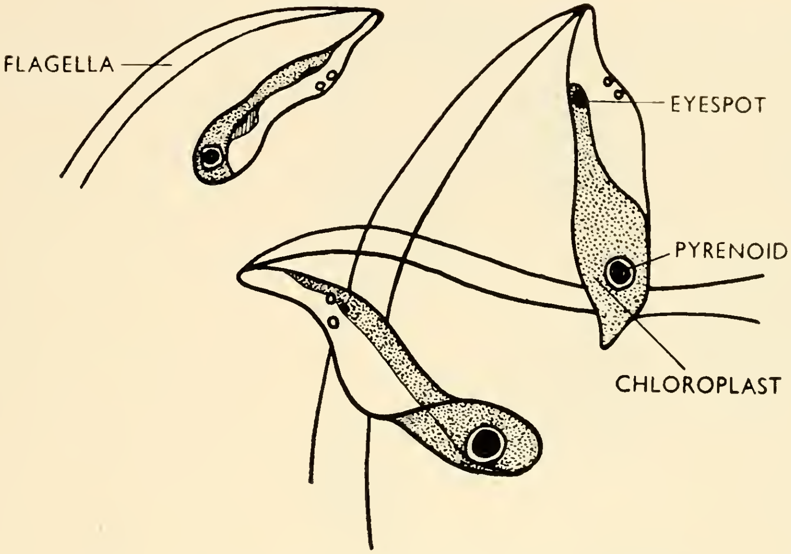


FIG. 51.—*Volvox rousseletii.* Mature antherozoids. (*After Rich.*)

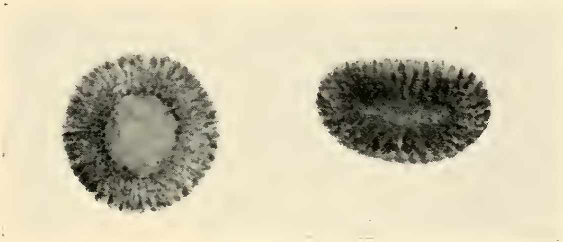


FIG. 52.—*Volvox aureus.* Two antherozoid clusters seen in surface and in marginal aspects respectively.

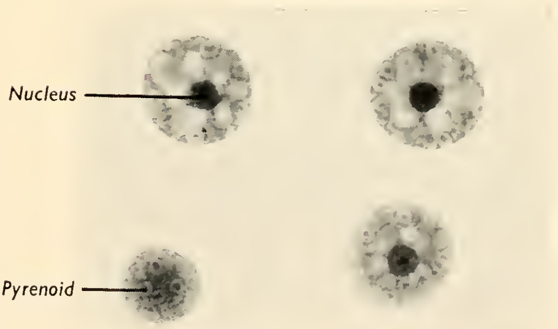


FIG. 53.—*Volvox aureus.* Young oospheres before fertilization.

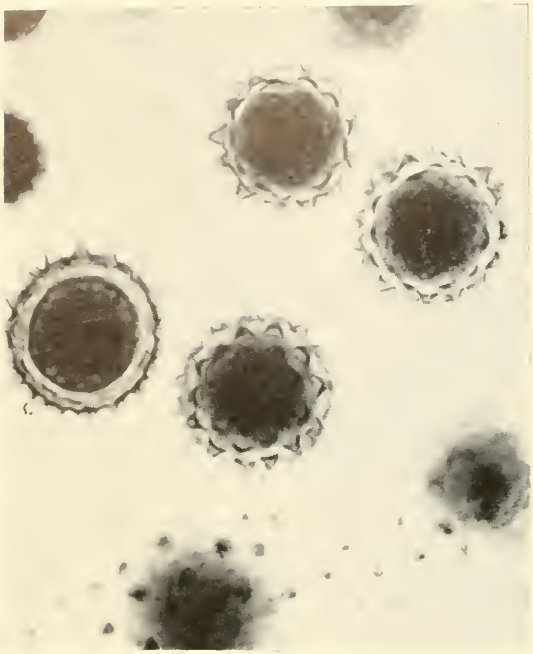


FIG. 54.—*Volvox aureus.* Mature oospores with spiny walls.

the interior of the parent sphere, and collectively may nearly fill it. They are eventually liberated by the breaking up of the parent colony (Figs. 48 and 49).

As these daughter colonies develop, the anterior or outer ends of the cells are directed inwards towards their respective centres. Shortly before their cells develop flagella the daughter colonies turn themselves completely inside out by a folding process which begins from the inner end, and thus restores the correct orientation of the cells (Fig. 50).

Sexual reproduction is of advanced type, with well-developed **oogamy.** The gametes may be produced either in distinct colonies or in the same one, either simultaneously or, more often, at different times. The **antherozoids** are biflagellate and fusiform, *i.e.*, spindle-shaped (Fig. 51). They have pale yellowish-green chloroplasts, and are developed in plates or circular masses (Fig. 52) formed by the division of the contents of specially enlarged cells. The female gametes or **oospheres** are rounded or flask-shaped and have no flagella (Fig. 53). They are contained in much enlarged cells of the colony, which are like the gonidia but larger. The oosphere often develops a kind of protrusion or beak, which is probably the point of entry of the antherozoid. After fertilization a spherical **oospore** is formed,

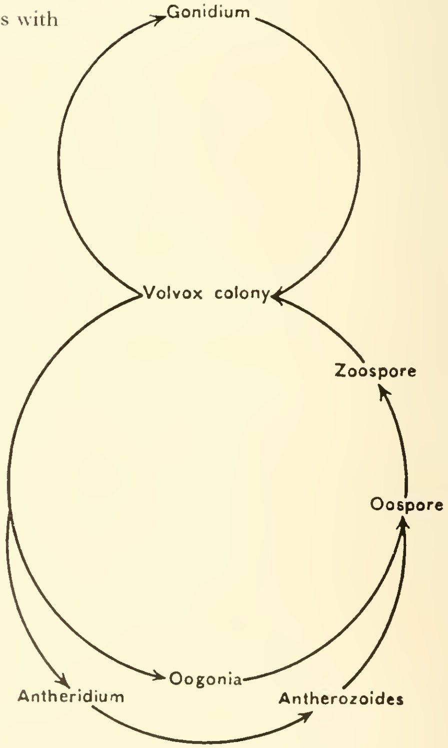


FIG. 55.—Life-cycle of *Volvox.*

with a smooth or stellate membrane and brownish-red contents (Figs. 53 and 54). It germinates to form a single monoploid zoospore, which by division gives rise to a new small colony which undergoes the usual eversion during its development (Fig. 55).

In the above examples we see the progressive development of the colonial type from the simple, unicellular *Chlamydomonas* to the highly complex colony of *Volvox*, with its very many component cells. We also see the gradual division of labour, from the condition in *Pandorina* in which all the cells of the colony are alike and able to reproduce, through *Eudorina*, in which there is a slight division of labour, in as much as the cells of the anterior and posterior ends show a difference in their morphology, to *Volvox* where there are specialized reproductive cells. We also see a tendency towards co-ordination, in the development of protoplasmic connections between the cells of the colony. We do not know the precise function of these connections, but it seems reasonable to suggest that they may in some way assist in controlling the movement of the complex colony of *Volvox*, and it is significant that the connections are more clearly developed in that type than in *Eudorina*, and that they have not been demonstrated in *Pandorina*. Another evolutionary tendency which we may notice in this series is the progressive elaboration of the sex organs. In *Chlamydomonas* the gametes are usually isogamous, in *Pandorina* they are anisogamous, while in both *Eudorina* and *Volvox* they are clearly differentiated into a small male gamete and a large female gamete which is fertilized without liberation, that is to say, is oogamous.

This *Volvox* series, as it is called, is interesting therefore, because by means of a few types we can illustrate apparent stages in an evolutionary series ; not, it is true, one which progressed very far, for it was apparently a side line culminating in *Volvox*, but one in which the present-day representatives of the various stages enable us to see the way in which this evolution took place. Its weakness seems to have been the retention of motility by the whole colony, since there are obvious mechanical limitations to progress along this line, and we shall see that all higher plants have evolved on the basis of retaining motility only for the reproductive cells.

Chaetophorales

The Chaetophorales are Chlorophyceae in which the thallus is divided into a flat, prostrate system of branched filaments attached to a substratum, and a projecting system of filaments which branch and grow upwards from the prostrate part. Such a thallus is said to be **heterotrichous.** The upright branches may develop hairs which are either composed of single cells or of rows of narrow elongated cells with scanty colouring matter. In *Coleochaete* they are merely outgrowths of the walls of the cells of the filaments and may be regarded as setae or bristles.

Reproduction is very variable. In many forms sexual reproduction is isogamous, with small motile gametes, in others it is oogamous, while in the most advanced members there is an elaborate alternation of sexual and asexual generations resembling more closely the Rhodophyceae than the Chlorophyceae. Asexual reproduction is either by means of zoospores or non-motile **aplanospores.**

The two types selected for special study may be regarded as representing the two extremes of the group. *Coleochaete* is the most elaborate, in fact its life history is in some ways more complex than that of any other Green Alga. *Pleurococcus*, on the other hand, is a very specialized but reduced form which has not only largely lost its filamentous character but also its reproductive mechanism, and relies on vegetative multiplication of cells by simple division.

It would be difficult to select any genus which might be said to be typical of the order as a whole, and it must be realized that neither of the types selected for detailed study fulfills that claim.

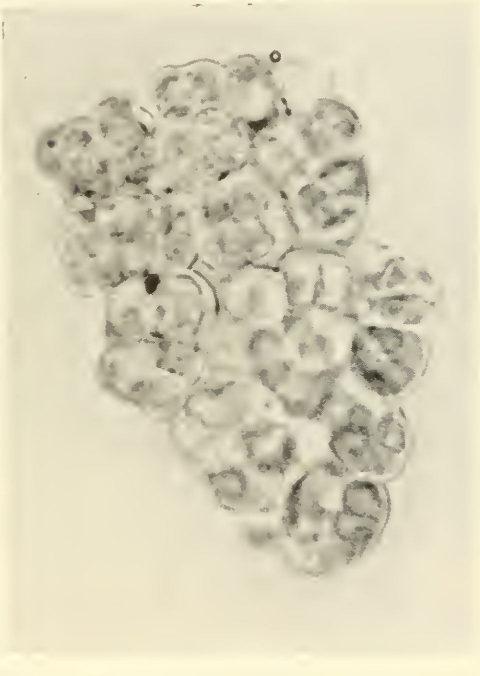


Fig. 56. *Pleurococcus naegelii.* A group of adherent vegetative cells, some showing cell division.

Pleurococcus naegelii

Pleurococcus is one of the commonest of the Algae found in terrestrial situations, occurring as a thin incrustation on the windward side of trees, stones, walls and palings. Probably no Alga has been subjected to more discussion as to its correct name. Frequently it is referred to as *Protococcus viridis* and also as *Chlorococcum vulgare*, while according to some workers its correct name is *Pleurococcus vulgaris*, though most authorities seem now agreed that it should be named *Pleurococcus naegelii*.

The structure is extremely simple (Fig. 56). The mature cells are sometimes isolated and more or less spherical, but they are more frequently found in groups of two, three, four or more, owing to their slow separation after division. In moist conditions there is a tendency for the cells to remain attached to one another and to elongate, with the result that short branched filaments are formed and such filaments readily arise when the Alga is grown in culture flasks.

Each cell (Fig. 57) is surrounded by a firm cell wall which is usually unthickened. The protoplast does not possess any obvious vacuoles and contains a hollow, spherical chloroplast with, on one side, an opening with a lobed margin. So large is this chloroplast that it seems to fill the cell, and it is only when the cell is in a suitable position that the lobing of the chloroplast can be seen. There is no pyrenoid present.

Reproduction

Reproduction is effected entirely by vegetative means ; by simple division followed by the separation of the cells. There is no evidence that this species possesses any special resting stage, for the ordinary cells are able to withstand long periods of desiccation without injury. The Alga can obtain what water is required directly from atmospheric moisture.

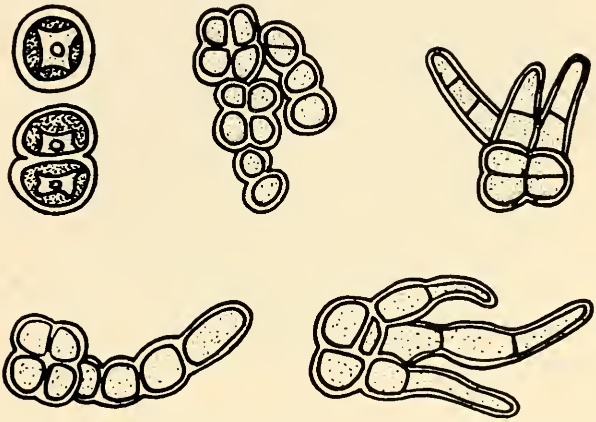


Fig. 57.—*Pleurococcus naegelii.* Various cell groupings showing the tendency to filament formation. (*After Fritsch.*)

Accounts have not infrequently been given of a motile stage closely resembling *Chlamydomonas* in appearance, with two apical flagella. Recent work indicates that such organisms are not part of the life-history of *Pleurococcus* but belong to other genera.

Coleochaete pulvinata

This Alga occurs not uncommonly in this country attached to the submerged leaves of water plants such as *Sparganium* and *Callitriche*, or to the fronds of *Lemna*. The thallus (Fig. 58) is green and heterotrichous, consisting of a flat prostrate part from which vertically growing filaments arise forming a cushion. Growth of the vertical filaments is apical, and of the prostrate part marginal.

The cells are all uninucleate and possess a single, large parietal chloroplast of irregular shape, with one or two prominent pyrenoids. Usually every cell bears a characteristically sheathed bristle which begins with the development of a pore in the outer cell wall, which is followed by the secretion of a membrane forming a tubular sheath extended outwards through the pore and attached to its margin. This sheath becomes impregnated with wall material and is soon indistinguishable from the wall itself. Its upper end becomes perforated, and a stream of cytoplasm passes out through the sheath, becoming homogeneous and solid, and forming the hair. Usually these hairs project at right angles to the surface of the thallus : later they may break off leaving only the sheath behind.

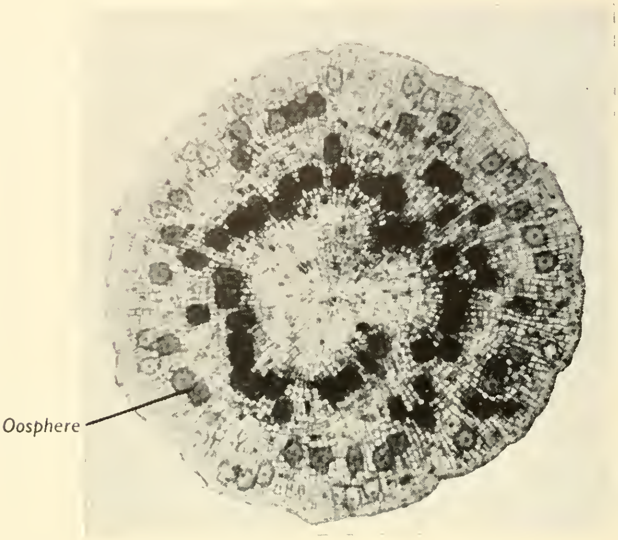


Fig. 58.—*Coleochaete scutata.* Female thallus with oogonia. In this common species, which is dioecious, no filaments are formed. Oogonia and antheridia are developed at the apices of radial cell rows, but are outgrown by the vegetative cells and remain embedded in the thallus, often forming concentric zones.

Asexual Reproduction

Asexual reproduction occurs chiefly in spring and early summer. Any cell of the thallus is capable of functioning as a **zoosporangium,** but most frequently it is the terminal cell of a filament which is involved. The contents round up to produce a single large, ovoid, biflagellate **zoospore** which frequently has a single laterally placed chloroplast ; it has no eye spot. After swimming for a while it settles down and divides. If the first division is horizontal the upper cell forms a hair, while the lower cell forms an embryo thallus ; if the division is vertical each segment grows out laterally as a thallus cell, but in either case the hair formation takes place at a very early stage.

Aplanospores, *i.e.*, non-motile spores, with fairly thick walls, may be developed from any cell of the thallus, one being produced from each cell.

SEXUAL REPRODUCTION

As has already been stated the sexual reproduction in *Coleochaete* is oogamous and shows an **alternation of generations** (Fig. 59). In fact it is

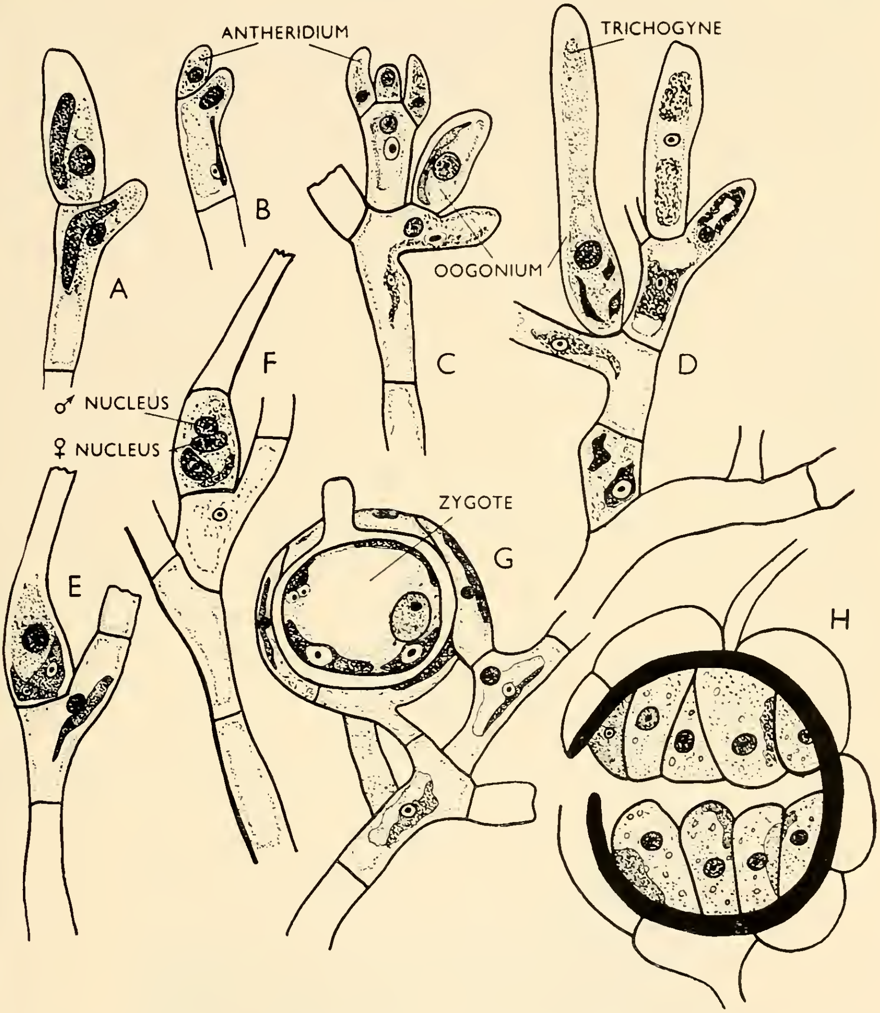


FIG. 59.—*Coleochaete pulvinata*. A, Young zoosporangium. B and C, Antheridial branch, with young oogonium. D, Oogonium shortly before the opening of the trichogyne. E, Oogonium after opening. F, Binucleate zygote. G, Enlarged oogonium with encircling filaments. H, Germination of the resting zygote (oospore). (*After Oltmanns.*)

the only example of a non-homologous alternation of generations in the Chlorophyceae, that is to say, an alternation in which the two generations are morphologically different. Sexual reproduction usually occurs from May to July.

The **antheridia** are developed in clusters at the ends of the vertically growing branches, frequently on the same branches that bear the oogonia.

They arise as small colourless outgrowths which become cut off from the parent cell. These antheridia are flask-shaped cells, each of which gives rise to a single, colourless, oval **antherozoid,** provided with a pair of apical flagella. The antherozoids are set free by the breakdown of the apex of the wall of the antheridium.

The **oogonium** is formed terminally on a short lateral branch from a vertical filament, but it is usually pushed into a lateral position by the upgrowth of a branch arising from the underlying cell. The oogonium is flask-shaped. The basal part is swollen and contains the chloroplast, while the neck is prolonged into a tube or **trichogyne,** which contains only colourless cytoplasm. When mature the tip of the trichogyne breaks down and some of the cytoplasm is extruded, while the basal part of the oogonium rounds off and forms a single **oosphere.**

Fertilization takes place by the antherozoid entering the trichogyne and passing down to the oosphere. The nucleus of the male gamete is considerably smaller than that of the female, but as the male gamete migrates towards the female nucleus, its nucleus increases in volume so that at the time of actual fusion the two nuclei are of approximately equal size.

After fertilization the oogonium enlarges, while the neck is cut off by a septum and a wall is laid down around the **oospore** so formed. This wall is thick and brown in colour and may be partly derived from the wall of the oogonium. Meanwhile new branches arise from the underlying cells of the branch bearing the oogonium, and grow around and envelop the oospore forming a pseudo-parenchymatous investment. These cells subsequently die and the oospore is shed enclosed both in its own wall and in that derived from the pseudo-parenchyma, which becomes fused to it. In this state it remains over the winter.

The following spring the contents gradually assume a bright green colour and divide (Fig. 60), first into two by a wall perpendicular to the long axis,

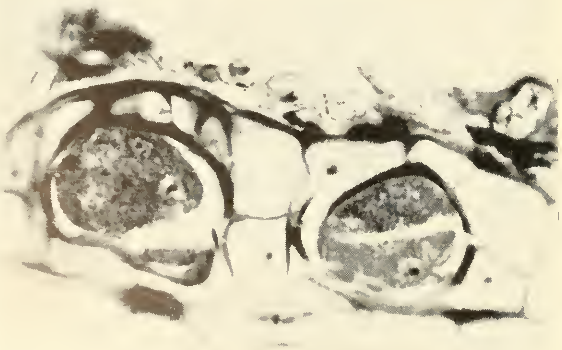


FIG. 60.—*Coleochaete scutata.* Sections through two germinating oospores showing division of the contents. The left-hand oospore shows stages of meiosis.

followed by a second division in the same plane and then by two walls at right angles to the others, cutting up the body into eight cells. Meiosis is said to take place during the first two divisions in this process so that this tissue formed within the germinating oospore is monoploid. By subsequent further cell division a wedge-shaped mass of sixteen or thirty-two cells is formed, by which time the oospore bursts open. From each of these cells a single zoospore develops and is liberated through the opening in the oospore wall. These zoospores are quite similar in shape to the zoospores formed in asexual reproduction. According to some workers they only give rise to asexual plants, and several asexual generations may be produced before the sexual plants reappear.

In the life-cycle of *Coleochaete pulvinata*, therefore, there is an alternation of sexual and asexual generations which is independent of the cytological alternations. All the vegetative individuals are monoploid, and the diploid condition is only maintained in the oospore, while the monoploid condition is again re-established during the germination of the oospore. We shall see later that this type of alternation of generations is remarkably similar to that in *Batrachospermum*. In fact there are a number of points of similarity between the sexual reproduction in *Coleochaete* and in members of the Nemalionales, though whether there is any justification for considering this to be indicative of any phylogenetic relationship is highly doubtful. It is generally regarded as an example of parallel evolution.

The life-cycle of *Coleochaete* may be represented by the following diagram :—

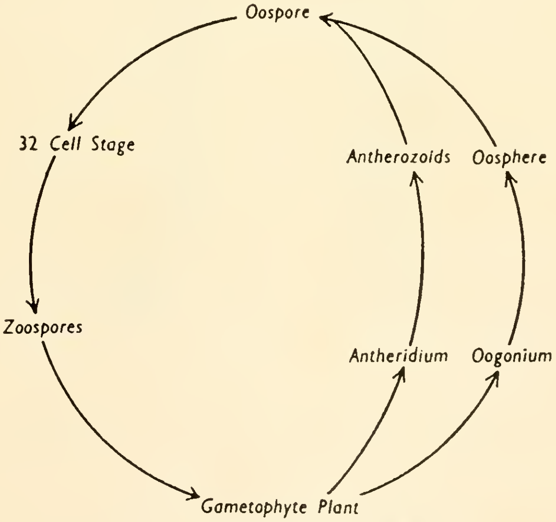


FIG. 61.—Life-cycle of *Coleochaete*.

It will be readily seen from this account that there is little or no obvious similarity between *Coleochaete* and *Pleurococcus*, and it is only on the grounds that *Pleurococcus* may occasionally form a filament of cells with an elongated terminal cell and the fact that it can produce a flat, prostrate cell mass, that a relationship is postulated. It will be realized, however, that *Pleurococcus* is highly reduced, as is indicated by the loss of sexual reproduction and motile zoospores.

Ulotrichales

The Ulotrichales are Chlorophyceae in which the cells are usually uninucleate and form simple or branched filaments. Asexual reproduction takes place by zoospores, or more rarely by non-motile spores. In the simpler members sexual reproduction is by isogametes. There is generally a single chloroplast in each cell which lies in close proximity to the wall and is therefore said to be **parietal.** The members of the group occur chiefly in fresh water.

Ulothrix zonata

This Alga is extremely common in running water and also in rain puddles. It is bright green in colour and consists of extremely fine filaments rarely exceeding one thousandth of an inch (0·025 mm.) in diameter (Fig. 62). These filaments consist of a single row of small cells, often as many as a thousand in a single filament. The threads are generally attached to stones, but they can live equally well when unattached.

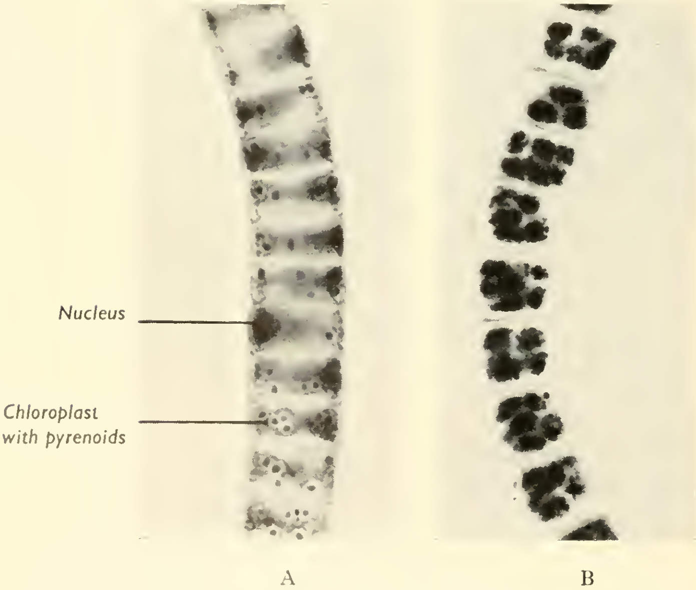


Fig. 62. *Ulothrix zonata.* A, Portion of a vegetative filament showing banded chloroplasts. B, Portion of a filament showing zoospores.

The cell has a cellulose wall, inside which is a lining layer of protoplasm in which the nucleus is embedded. The single **chloroplast** is in the form of a broad transverse band lying close against the wall and curved round the cell in the form of a ring. Situated in the chloroplast are several **pyrenoids.** The centre of the cell consists of a large vacuole containing cell sap.

In cases where the filaments are attached at the end, the anchoring cells are devoid of chlorophyll and are either brown or nearly white in colour. There is no special growing region and any cell of the filament may divide as elongation takes place. Vegetative multiplication is often effected by fragmentation of the filaments.

Asexual Reproduction

This consists in the formation of **zoospores.** They arise from the ordinary cells of the filament (Fig. 62, B), which divide up into a number of separate parts, generally from two to sixteen, though occasionally only a single zoospore may be produced from the mother cell. They are liberated into a delicate mucilage vesicle through a small aperture on one side of the cell.

The zoospores are of two kinds, **macrozoospores,** which are slightly flattened and have four flagella, and **microzoospores,** which are ovoid and have either four or two flagella. The latter type form an intermediate group between the macrozoospores and the gametes, and are not clearly distinguishable from the latter in appearance.

Each zoospore contains a single nucleus ; the chloroplast is situated in the broader part of the spore, while the apical end consists of clear protoplasm, attached to which are the flagella. There is a single contractile vacuole which pulsates about every ten seconds. Each zoospore is provided with an eye spot which is apparently sensitive to light. In light of moderate intensity they swim towards the source of light, but in very brilliant illumination they swim in the opposite direction. Finally, after swimming about for several hours, they come to rest, attach themselves and grow out directly into new filaments. On germination the first cell produced is a colourless rhizoidal cell attached to the substratum.

Sexual Reproduction

The gametes are produced either in cells of the same filaments as the zoospores or in different ones (Fig. 63). They resemble the microzoospores closely, except that each possesses only two flagella. Each mother cell divides to produce from eight to thirty-two **gametes.** Conjugation normally takes place only between gametes from different filaments. Fusion is similar to that described in *Chlamydomonas*, forming a zygote with four flagella. After fusion movement does not continue for long and soon the flagella are retracted and the zygote comes to rest, develops a thick wall and is transformed into a **zygospore.** It divides into a number of non-flagellated cells (**aplanospores**) which are liberated and form new filaments. The first division of the zygote is the reduction division, so that the cells of the filaments are monoploid.

We see, therefore, that in *Ulothrix* we have an example of perfect **isogamy,** in which the two gametes are of identical size and structure, though from the fact that gametes from the same mother cell will not fuse together we realize that there must be some physiological difference between them, which may explain why gametes of different origin are attracted to one another.

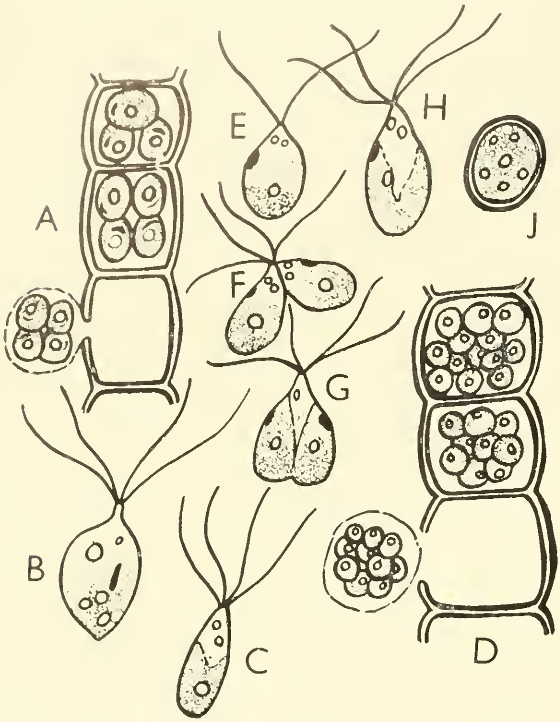


FIG. 63.—*Ulothrix zonata*. A, Release of zoospores from the cells of the filament. B, Macrozoospore. C, Microzoospore. D, Release of gametes. E, Gamete. F and G, Conjugation stages. H, Motile zygote. J, Zygospore.

Asexual reproduction in *Ulothrix* takes place chiefly in the winter, and it is at this time of the year that the growth of this Alga is most active. During the summer reproduction is by sexual means, and it is interesting to note that after the formation of the zygospore germination may proceed very slowly, and it may rest for a considerable period whilst still unicellular. It is only when conditions become more favourable that the new filament is produced. We see, therefore, that here, as in many other lower organisms, sexual reproduction may be associated with conditions which are unfavourable to vegetative growth.

Oedogoniales

The Oedogoniales are Chlorophyceae in which both the zoospores and the antherozoids are characterized by having a whorl of many flagella at their anterior end. Sexual reproduction is always of an advanced type ; the male organs, or antheridia, giving rise to antherozoids, and the female organs, or oogonia, each producing a single oosphere.

The vegetative cells are elongated and form a filament ; growth is by division of the cells, and in this process there is a characteristic annular splitting of the cell wall prior to the formation of the new cell. The filaments may be simple or branched.

We shall consider as our type the common Alga *Oedogonium*.

Oedogonium

Included in this genus are a large number of fresh-water species which frequently occur in ponds and tanks but are uncommon in running water. The Alga is composed of a filament of rather elongated cells, and is usually attached at one end by a rhizoid cell which is often expanded as a terminal disc or **holdfast.** This cell contains less chlorophyll than the other cells of the filament and is probably unable to assimilate food material.

The structure of the vegetative cell is simple ; it consists of a cellulose wall, bounding the inner surface of which is a layer of protoplasm. The centre of the cell is occupied by a large vacuole with cell sap. The chloroplast is a large cylindrical network, with several included pyrenoids formed from protein granules, around which starch grains are deposited. Embedded in the peripheral protoplasm of each cell is a single large nucleus.

Growth consists in the division of the cells of the filament. The apical cell does not divide, and in some species is elongated as a fine slender terminal hair. Only certain cells of the filament divide, and these are distinguished by the formation of an internal ring on the wall, near the upper end (Fig. 64).

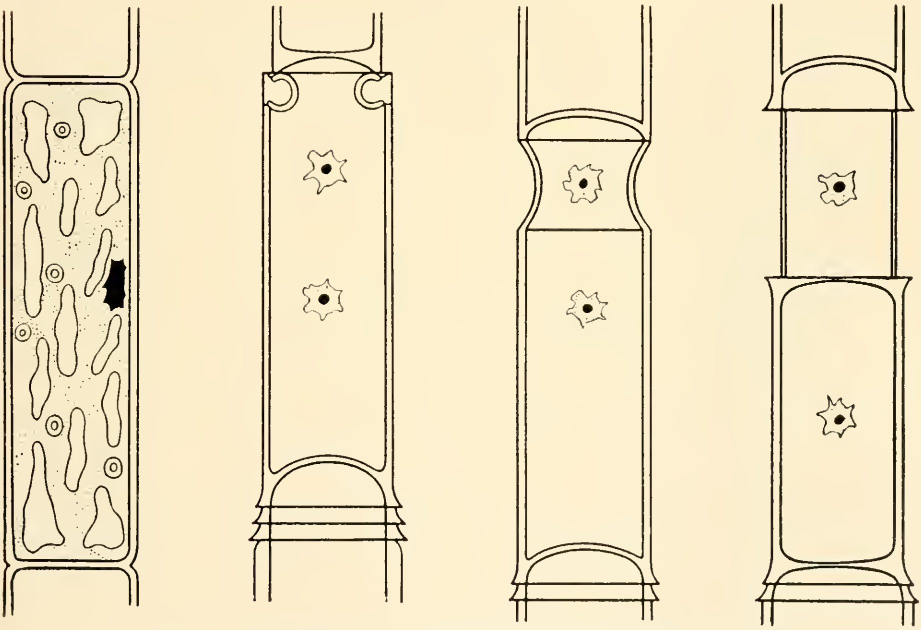


Fig. 64.—*Oedogonium sp.* Vegetative cell on left. Stages in cell division on right with nuclei only shown. (*After Hirn.*)

The cell divides transversely and then the cell wall splits at the level of the ring, which stretches out longitudinally to form a new portion of cell wall. Another ring then forms at the upper edge of this new length of wall. Only the cell which contains the ring divides again, and it possesses overlapping caps at its upper end, each marking the position of a ring and equal in number to the times the cell has divided. The occurrence of these **cap cells** in the filaments makes *Oedogonium* easily recognizable.

Reproduction is both sexual and asexual, the latter occurring during the summer months under conditions favourable for growth, while the former, since it results in the production of resting spores, is suitable for tiding the Alga over periods unfavourable for growth, such as, for example, drought.

Asexual Reproduction

In asexual reproduction any cell of the filament may function. The protoplast is withdrawn from the cell wall and forms a mass in the centre of the cell (Fig. 65). One area at the side of this mass becomes colourless and round this numerous fine flagella are developed. The cell wall splits across and the protoplasmic mass passes out through the opening. On being liberated the **zoospore** slips out of the gelatinous membrane which originally surrounded it and becomes spherical. There is no true wall around the zoospore, for the whole mass is purely protoplasmic in structure. It swims by means of the flagella, possesses an eye spot and is sensitive to light in just the same way as we have described in the case of *Ulothrix*. After swimming for an hour or so it settles down on its colourless end, withdraws its flagella and secretes a cell wall. The free end grows out and is divided by a transverse wall, thus beginning a new filament. The colourless portion usually develops into the branched **holdfast cells.**

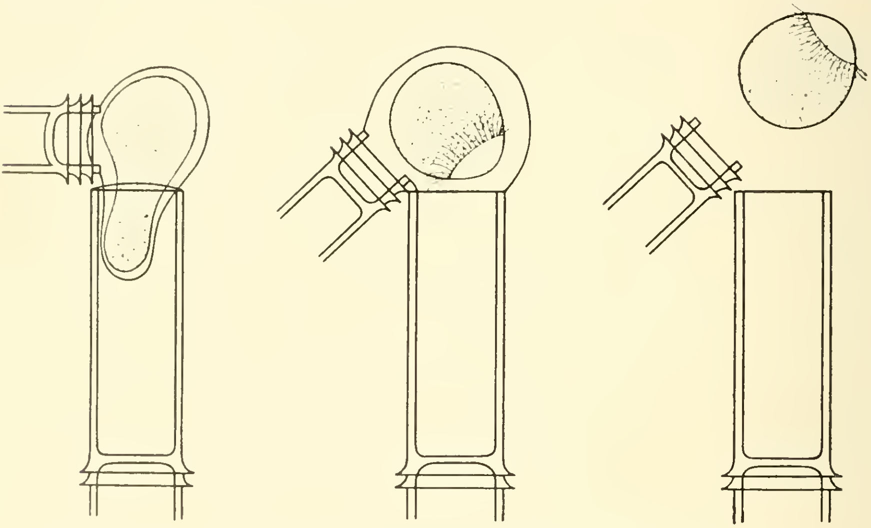


Fig. 65.—*Oedogonium concatenatum*. Stages in the liberation of a zoospore. (*After Hirn.*)

Sexual Reproduction

The sexual reproduction of *Oedogonium* is of an advanced and complicated type. The distribution of the sexes varies in the different species. In some both sexes occur in the same filament, when it is said to be **monoecious,** while in others the male and female organs are borne on different filaments, and the plants are spoken of as **dioecious.** The male cells are formed by repeated transverse divisions of a vegetative cell, which in monoecious species is close to the female organ. These divisions continue until a row of about a dozen small cells are produced, each of which is termed an **antheridium.** The contents of each antheridium divide into two, and each portion becomes an **antherozoid.** These antherozoids resemble the zoospores, but are much smaller.

The female organ, or **oogonium,** is formed from a single vegetative cell which divides into two, the upper cell being much richer in protoplasm than the lower one. It has a large nucleus and forms the oogonium, while the lower cell is termed the **supporting cell.** The oogonium swells out to about twice its original diameter and becomes rounded or oval in outline. The cell contents are withdrawn from the wall and form a free, rounded, protoplasmic body or **oosphere.** A small clear patch appears on one side, which is called the **receptive spot.** The wall of the oogonium now opens either by a split or by a thinning of the wall above the receptive spot, and is thereupon ready for the entry of the antherozoid.

In addition to the normal monoecious and dioecious types, certain dioecious forms of *Oedogonium* are known in which the male filaments are very much smaller than the female. Such plants are spoken of as **dwarf male** or **nannandrous** forms. Cells of the parent filament divide by repeated transverse division, and from each of the cells formed a single zoospore escapes. It is intermediate in size between the asexual zoospores and the antherozoids and is termed an **androspore.** The androspores swim till they reach the female filaments, attaching themselves either to the oogonium itself or to a cell close to it. Here they germinate and produce a filament of two or three cells. With the exception of the lowest, which forms a holdfast, each becomes an antheridium liberating two antherozoids (Fig. 66).

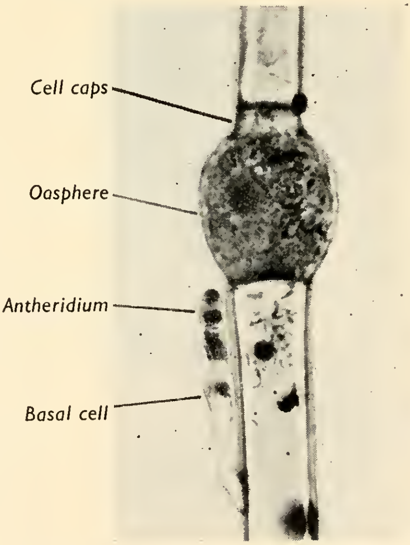


Fig. 66.—*Oedogonium sp.* Reproductive organs of a nannandrous species showing a dwarf male plant attached below the oogonium.

Fertilization is effected by the entrance of the antherozoid through the opening in the wall of the oogonium, after which it unites with the oosphere.

After fertilization the oosphere secretes a thick wall and is now known as an **oospore.** The contents of the oospore undergo considerable change ; the green colour disappears and is replaced by a brown or red pigment, while large quantities of oil appear in the protoplasm. Such a structure is regarded as a **resting spore,** and it may remain for a considerable time in this condition before germinating. It is thus an extremely suitable structure for tiding the Alga over a period of unfavourable conditions.

When conditions are favourable for its germination the cell wall bursts and the contents slip out surrounded by a thin membrane. It now normally divides by meiosis into four monoploid cells, and from each of these a flagellated zoospore is produced exactly resembling the asexual zoospores. These zoospores free themselves from the membrane and swim away, giving rise eventually to separate plants.

In *Oedogonium*, then, we have an example of a green Alga, with an advanced type of sexual reproduction as compared with *Ulothrix*. Its method of sexual reproduction is in some respects comparable with that of the higher plants, but it is peculiar in the production of nannandrous male filaments.*

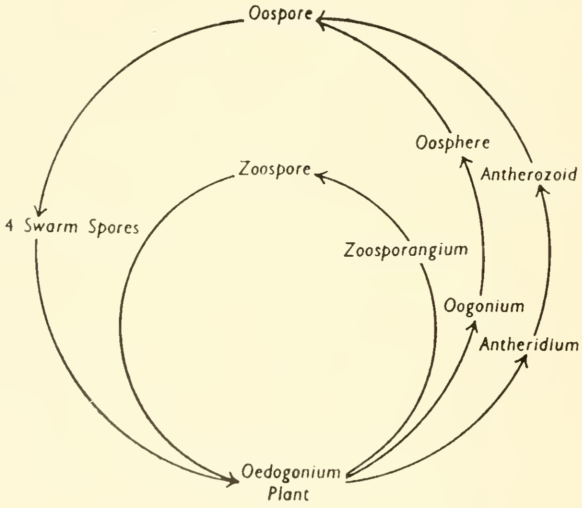


FIG. 67.—Life-cycle of *Oedogonium*.

Despite the fact that it is itself highly evolved, it is doubtful if *Oedogonium* is related to any higher type of plant. It would appear rather that it is an end line, specialized along certain directions, but not along those which produced the higher forms of plant life (Fig. 67).

Conjugales

The Conjugales are Chlorophyceae devoid of flagellated reproductive bodies. Sexual reproduction is by means of amoeboid gametes. Asexual

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* Similar dwarf male plants are found in some species of mosses.

reproduction is unknown. The vegetative cells are generally large, and possess large, elaborately shaped chloroplasts. The plants may be unicellular or the cells may be united together into filaments, which may fragment into separate unicellular parts.

Included in this group are the Desmids, which are among the most beautiful of the Green Algae. Most of them are unicellular, but the wall of the cell is divided into two halves, or **semi-cells,** each of which is often extremely complex in outline and is connected to the other by a narrow region called the **isthmus.**

We shall consider only one type of the Conjugales, *Spirogyra.*

Spirogyra

Spirogyra is a very common bright-green Alga which may be found in large masses growing in ponds and slow-flowing rivers. The filaments are usually free, but are sometimes attached at one end to a substratum by a branched and colourless rhizoidal cell or **holdfast.** These masses are very slimy to the touch, owing to a mucous sheath surrounding the cells, and consist of enormous numbers of long, unbranched, green filaments.

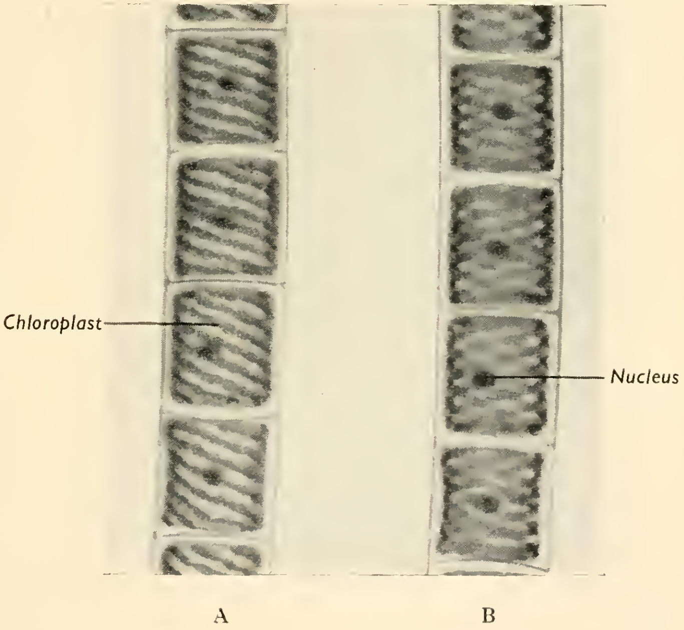

Fig. 68.—*Spirogyra sp.* Vegetative structure of filament. A, Surface view. B, In optical section.

There is no morphological differentiation between the cells of the filament (Fig. 68). A delicate sheath of cuticle surrounds the entire filament inside the mucous sheath, while each cell has its own polysaccharide wall, inside which is a peripheral layer of cytoplasm. The central part of the cell is occupied by a large vacuole containing cell sap. The nucleus is suspended in the centre of the vacuole by cytoplasmic strands. The most conspicuous structure in the cell is the chloroplast, which consists of one or more spiral bands lying in the peripheral layer of cytoplasm. It is the appearance of these bands that has given the plant its name. Embedded along the chloroplast are numerous pyrenoids around which is stored up the starch acquired during photosynthesis. In section the chloroplast is usually T-shaped, the inner flange being connected by fine filaments of cytoplasm to the nucleus.

The filaments grow by simple cell division, each cell dividing by a wall transverse to its length, and any cell of the filament being capable of division. Such a type of growth, where any cell of the filament can divide, is spoken of as **intercalary growth,** and may be contrasted with the **apical growth** of higher plants, where division is restricted chiefly to the cells of the growing point.

Cell division in *Spirogyra* begins before nuclear division, not after it as in higher plants, and the two processes are completed simultaneously. The new transverse wall starts as a ring on the inner surface of the longitudinal walls and grows inwards towards the centre. The cell does not necessarily divide into two equal parts, for the new wall lies exactly half-way between the nuclei, wherever that may happen to be in the cell. The position of the new wall is therefore fixed by the position of the nuclei and this position is determined while the mother nucleus is still in the metabolic condition. A similar condition exists in *Cladophora*.

Nuclear division in *Spirogyra* is also exceptional in that the nuclear membrane persists and divides with the nucleus, the spindle being formed inside the nucleus instead of in the cytoplasm.

SEXUAL REPRODUCTION

Spirogyra grows in dense masses, and in this condition the filaments at the time of sexual reproduction come to lie side by side, probably as a result of surface tension changes. In this position sexual reproduction is possible by a process known as **conjugation** (Fig. 69). Most frequently this process takes place in the spring, but it can be induced by the presence of a liberal supply of sugar, or by a deficiency of nitrogen. The filaments adhere closely to one another in pairs surrounded by a common investment of mucilage, and then, preliminary to conjugation, opposite cells in adjacent filaments develop short protuberances from their side walls, which are in contact with each other from the start, and as they grow push the filaments apart. Each pair of protuberances when united forms a **conjugation canal.** The wall between them partially breaks down and a small **conjugation pore** is formed, through which the protoplasts of the two opposite cells come into contact. Conjugation by this method is called the **ladder type** from the appearance of the two parallel filaments linked by the conjugation tubes. At this stage the mucous sheath of the filaments disappears.

Meanwhile the contents of the conjugating cell which is about to function as the male gamete contract away from the outer cell wall but without losing contact with the female. In this process many contractile vacuoles are formed, which pump water from the central cell vacuole into the space between the cell wall and the contracting cytoplasm. Subsequently the female gamete also contracts from the conjugation tube, leaving a space into which the male gamete passes, enters the other cell and fuses with the female gamete. It appears that the migration of the male gamete along the conjugation tube and the contraction of the female are brought about by the pumping action of contractile vacuoles. In *Mougeotia* and certain allied genera the process is slightly different, both gametes passing into the conjugation tube, where the zygote is formed. Such types are therefore isogamous.

The active gamete is looked upon as the male and the passive one as the female, although they do not show any morphological differences. We have therefore here a case of physiological heterogamy. In some species of *Spirogyra* all the male gametes are formed in the cells of one filament, and all the females in the other, with the result that after conjugation we find one filament entirely devoid of cell contents, while the other contains all the zygotes. In other species some cells function as males and others as females, with the result that the zygotes are distributed between both filaments. The former species are dioecious and the latter are monoecious.

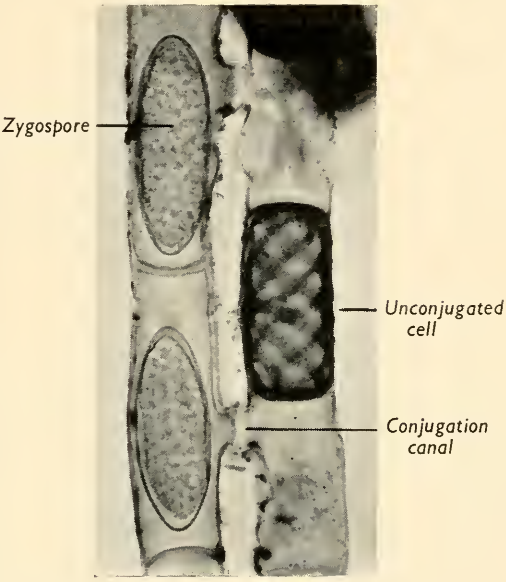

FIG. 69.—*Spirogyra sp.* Sexual reproduction, ladder type. Two completed zygospores appear in the left-hand filament. In the right-hand filament one cell has remained unpaired.

There is also another type of conjugation called the **chain type,** in which adjacent cells of the same filament unite through tubes which are formed like side-links between cell and cell. In this case alternate cells behave as males and females respectively, and there is no sexual differentiation between the filaments as a whole. In some species this method is the rule.

Whatever the position of the formation of the zygote its subsequent development is the same. Immediately after the fusion of the gamete nuclei a **zygospore** is formed. A zygospore is a zygote enclosed in a thick wall. It is specially adapted for withstanding dry conditions, and is easily recognized by the thick yellow-brown wall which is usually produced. In *Spirogyra* the wall consists of three distinct layers, the characteristic chloroplast disappears and the cell becomes filled with brownish oil-drops.

The further development of the zygospore depends upon the decay of the parent filament. As this consists simply of the dead cell wall, its decomposition in water is fairly rapid, and in time the zygospores are set free and fall to the bottom of the pond. Activity only begins when the zygospore is lying in water : it will not germinate in a dried-up pond. Under suitable conditions the thick wall is burst open and the contents emerge as a green cell which divides transversly, the lower half forming a rhizoidal cell, while the upper half divides repeatedly to form a new filament (Fig. 70). At the beginning of germination the nucleus of the zygospore divides into four by meiosis, but only one of the four monoploid nuclei survives, to become the nucleus of the first cell of the new plant.

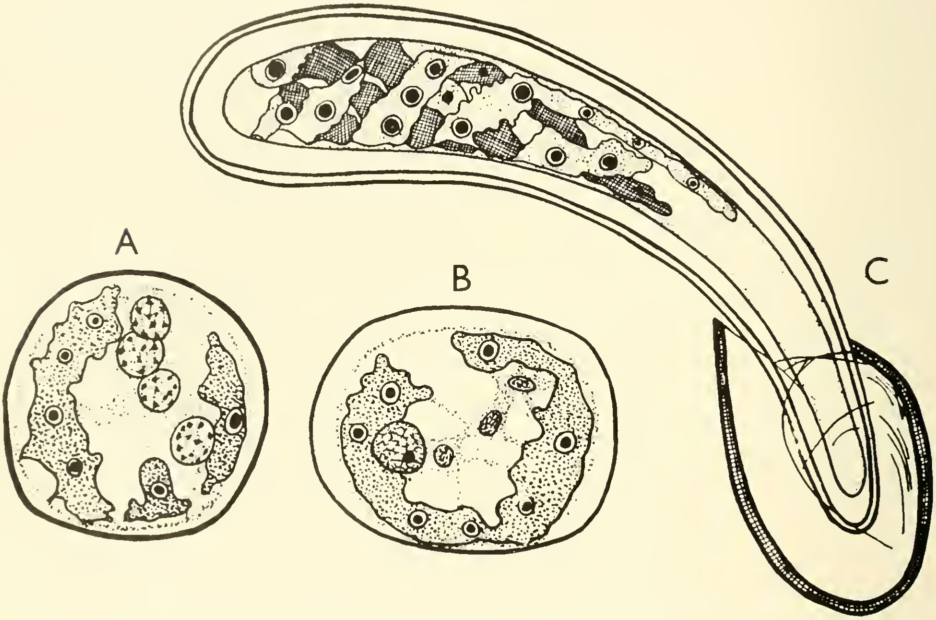

Fig. 70.—*Spirogyra longata.* A, Nuclear division in the zygospore. B, Abortion of three of the four nuclei formed. *S. neglecta.* C, Germination of the zygospore. (*After Tröndle.*)

There is no asexual method of reproduction in *Spirogyra*, and this and the entire absence of any truly motile gametes constitute the fundamental characteristics which distinguish this genus, as well as the whole of the Conjugales, from the rest of the Green Algae. It seems probable that the absence of motile gametes is a feature associated with the habit of the plant of living in dense masses where little or no difficulty is experienced in the association of cells potentially able to conjugate, as a result of which the gametes have, in the course of evolution, lost the power of motility.

Spirogyra has, however, a method of multiplying vegetatively by the fragmentation of the filaments into single cells, each of which becomes the starting point of new growth. In many species this process, which occurs mostly in early spring, is assisted by the action of a ring-like fold on the end walls of the cells, somewhat like that in *Oedogonium*, which expands laterally and thus ruptures the cuticular sheath of the filament.

Although the filaments of *Spirogyra* are multicellular they are not, biologically speaking, individuals, but rather colonies of comparatively independent cells. At sexual reproduction they behave like unicellular types in that the conjugating units are used up and disappear as such. This limits the reproductive capacity of the plant in comparison with higher forms in which a vegetative body persists and may reproduce many times (Fig. 71).

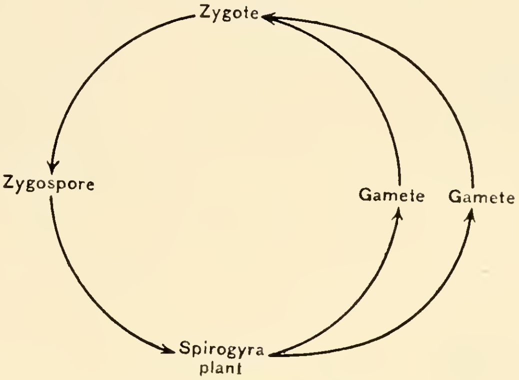

FIG. 71.—Life-cycle of *Spirogyra*.

Siphonales

The Siphonales are Chlorophyceae in which the thallus consists of a single multinucleate cell or **coenocyte,** which often grows to form a structure of macroscopic size. Asexual reproduction occurs in a few genera by the formation of zoospores. The sexual reproduction in many of the marine genera is by the fusion of unlike motile gametes ; that in the fresh-water genera is oogamous.

Some of these coenocytic Green Algae show great complexity. For example, in the genus *Caulerpa*, there is a complex development of coenocyte branches to form a thallus, which may be as much as 10 cm. in height, with a definite external form. The thallus in *Caulerpa* is especially remarkable, since the branches of the single coenocyte build up thalli that simulate in appearance the differentiation into roots, stems and leaves found in the higher land plants (Fig. 72).

We shall consider two types of the Siphonales, *Bryopsis* and *Vaucheria*.

Bryopsis plumosa

The genus *Bryopsis* is distributed mainly in tropical seas, but one species, *B. plumosa*, is commonly found in spring and early summer on the British coasts. The thallus consists of a single coenocyte, but this enormous cell shows differentiation into a **main axis**, from which arise, towards the upper end, two rows of lateral branches or **pinnae** (Fig. 73). From the lower end of the axis there is formed a little-branched horizontal rhizome anchored by rhizoids. This rhizome may produce numerous upright axes, so that each plant actually consists of a little tuft of vertically growing filaments. The pinnae vary in length, those nearest the base being the longest and decreasing regularly towards the apex. Each pinna is an elongated sac, and there is a constriction at the base where it joins the main axis (Fig. 74). No true septa are formed in the coenocyte prior to the reproductive phase and the

FIG. 72.—Various species of *Caulerpa* illustrating the remarkable degree of differentiation which can be achieved by a coenocytic structure. A, *C. ligulata.* B, *C. clavifera.* C, *C. prolifera.* D, *C. sertularioides.*

entire plant has one continuous vacuole lined by cytoplasm and containing numerous minute, round chloroplasts and nuclei.

FIG. 73.—*Bryopsis plumosa.* Form of the whole plant.

Vegetative propagation may be effected by the detachment of pinnae which become plugged at the point of abstriction. These are able to develop new rhizoids and grow into fresh plants. It is interesting to note that in conditions of dull light or when plants are placed upside down the apices of the pinnae develop rhizoids.

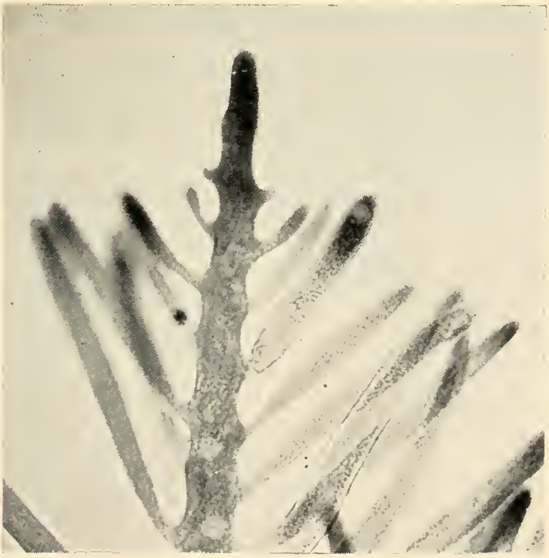

FIG. 74.—*Bryopsis plumosa.* Enlarged tip of thallus showing the growing apex and the coenocytic structure.

The only known method of reproduction is by means of gametes. There is no asexual method of reproduction.

Sexual Reproduction

The gametes are not alike and are usually produced on separate plants. The first stage consists of the cutting off of a pinna from the main axis by means of a septum which arises as a ring-like thickening. The whole of the pinna thus forms a **gametangium** whose protoplasmic contents increase and the chloroplasts multiply by division. In the male gametangium the pyrenoids disappear from the chloroplasts, but they remain in those of the female gametangium. Later the contents divide up by simultaneous cleavages to form gametes (Fig. 75), which are liberated by the gelatinization of the apex of the pinna. The gametes are pyriform with two equal, apical flagella. The female gamete is about three times as large as the male and is provided with a deep-green chloroplast. In the male the chloroplast is yellowish in colour and probably not functional. Gametes fuse in pairs and produce a zygote which may, for a time retain all four flagella. Later it rounds off and germinates directly to produce a new plant. The plants are diploid and reduction division occurs in the formation of the gametes (Fig. 76).

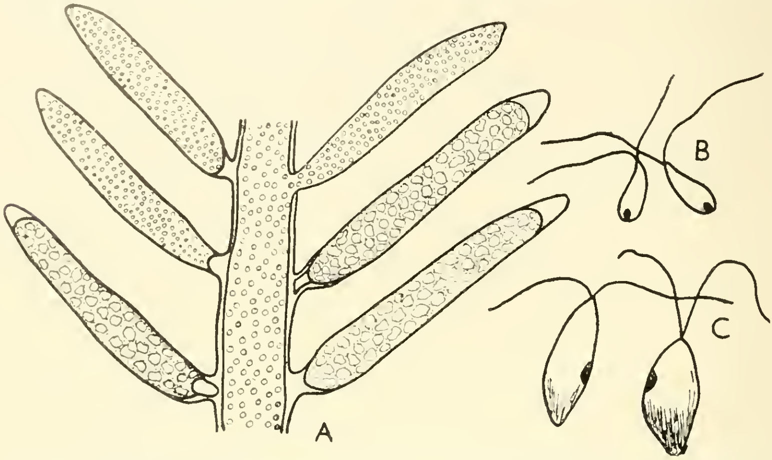

Fig. 75.—*Bryopsis cupressoides*. A, Branches of the thallus forming gametangia. B, Male gametes. C, Female gametes. (*After Oltmanns.*)

Vaucheria

This Alga is largely terrestrial, occurring frequently on damp soils, as, for example, on the soil in flower pots, where it forms a green felt-like covering. It may also be found in fresh water, and it is under these conditions that asexual reproduction most frequently occurs.

Vaucheria consists of an non-septate, tubular coenocyte with lateral branches. It is dark green in colour and is very sensitive to changes of environment. The coenocyte is frequently attached to the substratum by means of a branched holdfast or **hapteron,** which may be brown or white in colour and is devoid of chloroplasts. The remainder of the coenocyte contains a lining layer of protoplasm closely applied to the cell wall, and in it are embedded numerous nuclei and chloroplasts. The central part of the coenocyte consists of a vacuole containing cell sap. The chloroplasts are small and discoid, but in some species they become spherical when exposed to intense light.

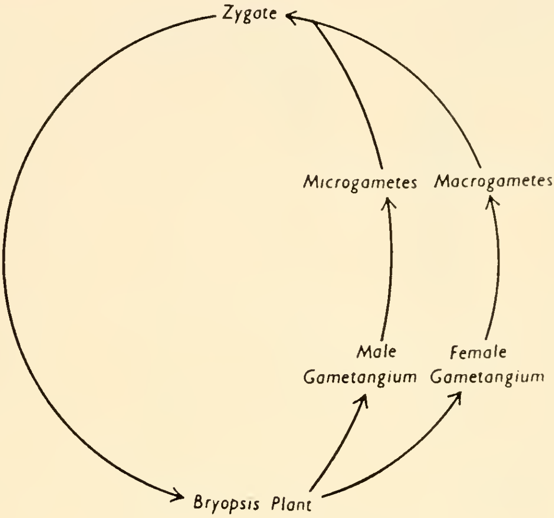

FIG. 76.—Life-cycle of *Bryopsis.*

In *Vaucheria* the reserve material is oil, which is stored in countless tiny droplets in the cytoplasm. Under normal circumstances no starch is formed, but under constant intense illumination it can be produced, which seems to indicate that the appropriate enzymes are present.

Injury to the thallus results in the formation of a septum sufficing to isolate the injured part, but otherwise, with the exception of those formed in relation to the sex organs, no septa occur.

ASEXUAL REPRODUCTION

Asexual reproduction takes place by the formation of **zoospores** (Fig. 77), which are produced singly in club-shaped **zoosporangia.** The sporangia develop singly from the swollen ends of the branches by the accumulation of a large amount of cytoplasm with many nuclei and chloroplasts in the swollen tip, which, as a result, diminishes the size of the central vacuole, and thus these tips appear dark green in colour. Inside the zoosporangium a single large mass is formed which is termed the **zoospore.** It contains many nuclei which are arranged in a single layer near the surface and opposite each nucleus a pair of flagella is developed. The zoospore is liberated by the breakdown of the apical part of the wall of the sporangium to form a small pore through which the large zoospore forces its way. This zoospore is generally interpreted as a compound structure, resulting from the failure of the protoplast within the sporangium to divide into a number of uninucleate biflagellate zoospores. Zoospores are formed only by aquatic species or by terrestrial ones which have become flooded. They are usually developed during the night, or they may be induced by a sudden transference from light to darkness, or from running to quiet water. On liberation the zoospores are sluggish and only swim for a short time. On coming to rest the flagella are immediately withdrawn and a thin membrane is secreted around the zoospore. Germination begins with the protrusion of two or more tubular outgrowths, one of which attaches itself to the substratum and forms the holdfast, whilst the other produces the filament.

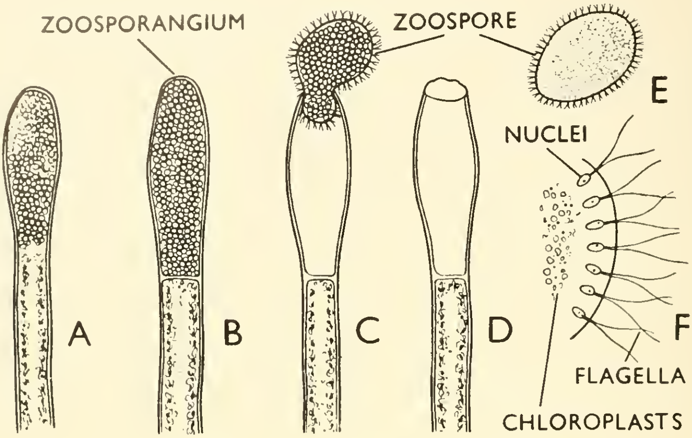

Fig. 77.—*Vaucheria repens.* A to D, Formation of the zoosporangium and liberation of the zoospore. E, Liberated zoospore. F, Structure of the periphery of the zoospore. (*After Goetz.*)

Not all species of *Vaucheria* produce zoospores. Some develop what are termed **aplanospores.** These are simple non-flagellate structures which are produced in special sporangia called **aplanosporangia.** These aplanosporangia develop as swellings either on the main or lateral branches of the thallus. When mature the aplanospores simply drop out of the aplanosporangium through a perforation in the wall. This second method of asexual reproduction occurs most commonly among terrestrial species.

Sexual Reproduction

In *Vaucheria* the sexual reproduction is oogamous and occurs most frequently in plants growing on damp soil or in quiet water, but is rarely found in plants growing in streams. The **antheridia** and **oogonia** are borne close to one another, either together on the same filament or on a common lateral branch or on adjoining lateral ones. Development of the oogonium begins (Fig. 78) with the formation of a swelling, which becomes filled with

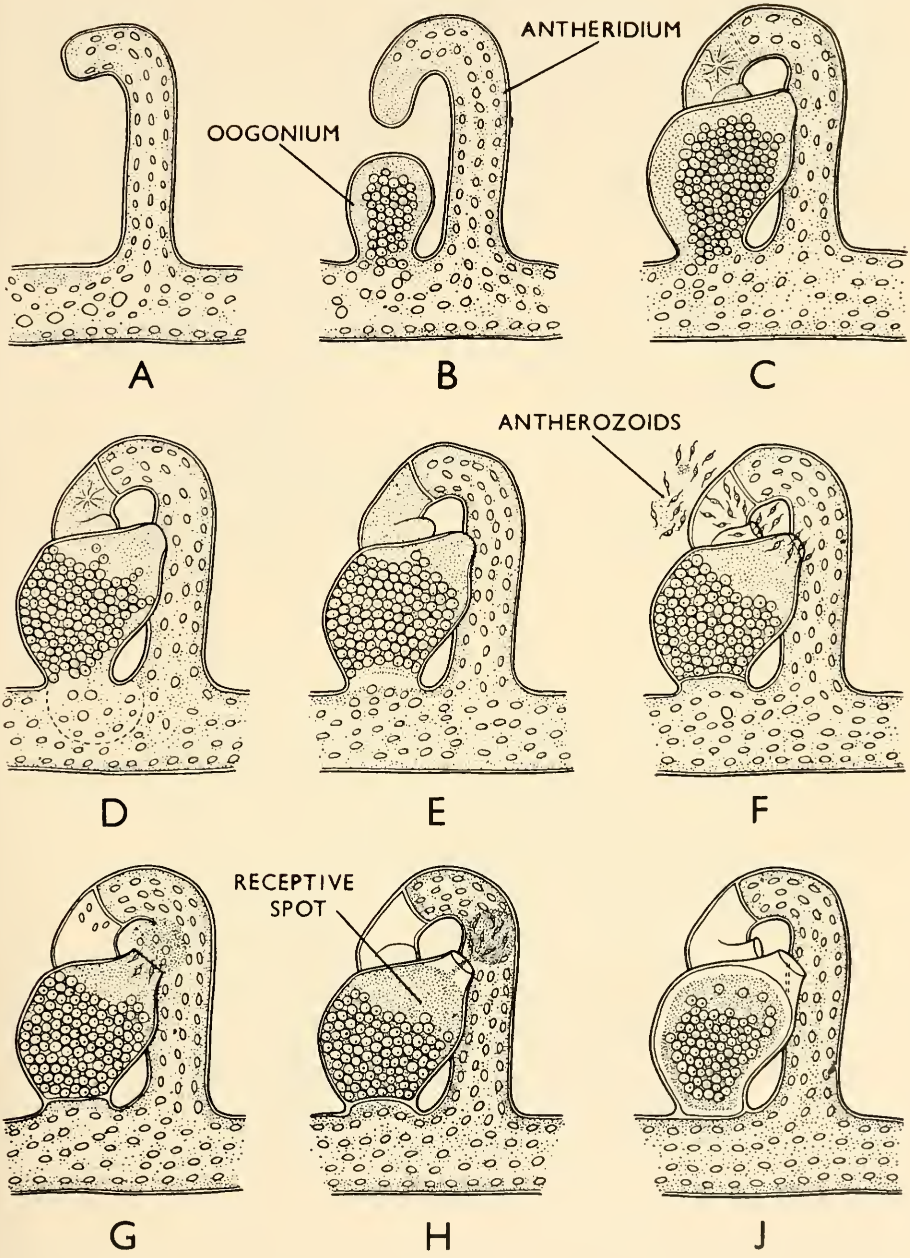

FIG. 78.—*Vaucheria sessilis*. A, Young antheridium. B, Antheridium and young oogonium. C, Antheridium with septum and oogonium with developing beak. D and E, Protoplasm returning from oogonium into filament. F, Liberation of antherozoids, oogonial beak open, oogonium septate at base. G, Exudation of cytoplasm from oogonial beak. H, Fertilization stage, antherozoids in extruded cytoplasm. J Oospore membrane formed after fertilization. (*After Couch.*)

nuclei, oil and chloroplasts, though ultimately only a single central nucleus remains, which reaches a considerable size. The rest migrate back into the filament. The whole oogonium then becomes cut off from the rest of the coenocyte by a transverse wall or septum. Later a **beak**, or lateral swelling, is developed at one side of the oogonium, and in this region the wall becomes gelatinous and dissolves, leaving a pore. It is at this point that, subsequently, the antherozoids enter the oogonium. When mature the chloroplasts and oil take up a central position, leaving either a clear peripheral area of protoplasm or at least a clear area under the beak, the **receptive spot,** and the contents as a whole contract and become the **oosphere** (Fig. 79).

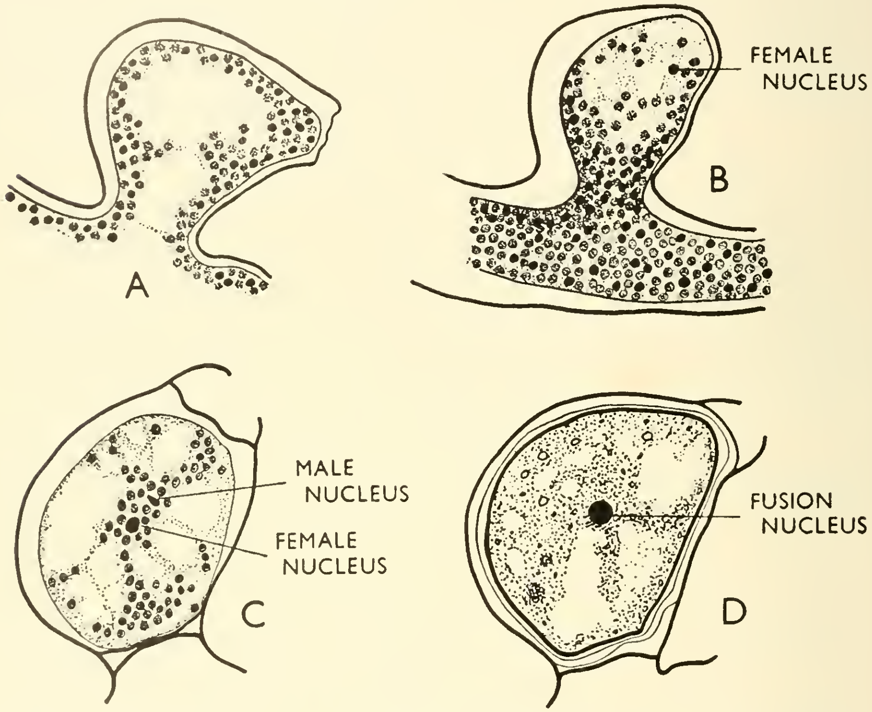

Fig. 79.—*Vaucheria sessilis.* Maturation of the oogonium. A, Young stage. B, Nuclei returning from oogonium to filament. C, Oosphere at fertilization stage. D, Oospore. (*After Oltmanns.*)

The **antheridia** are formed at the ends of short lateral branches and develop simultaneously with the oogonia (Fig. 80). Each antheridium is an elongated, strongly curved structure and is cut off from the thallus by a septum. The nuclei within the antheridium divide up and ultimately each becomes surrounded by a small mass of cytoplasm and constitutes an **antherozoid.** These antherozoids form a mass in the centre of the antheridium, whilst the periphery is filled with chloroplasts and residual cytoplasm. The antherozoids are liberated apically shortly before daybreak, as very minute, colourless, oval bodies with two laterally inserted flagella.

At the time of fertilization (Fig. 81) the oosphere exudes a droplet of gelatinous cytoplasm through the pore in the oogonium wall, and the antherozoids accumulate in numbers around the droplet. Several antherozoids may enter the oogonium, but only one enters the oosphere. The small male nucleus migrates to that of the oosphere, which is considerably larger, but does not immediately fuse with it. Whilst lying side by side the male nucleus increases in size, and when its volume equals that of the female nucleus the two fuse together.

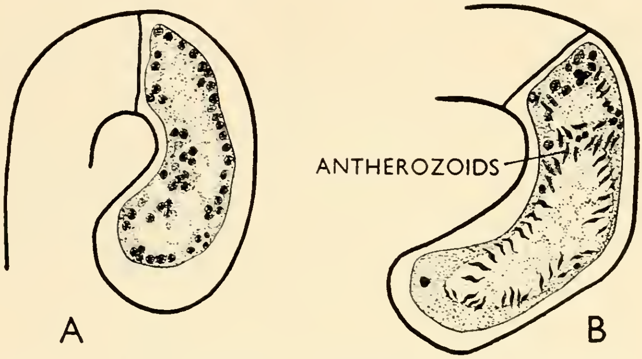

Fig. 80.—*Vaucheria sessilis.* Development of the antheridium. A, Young stage. B, Differentiation of antherozoids. (*After Oltmanns.*)

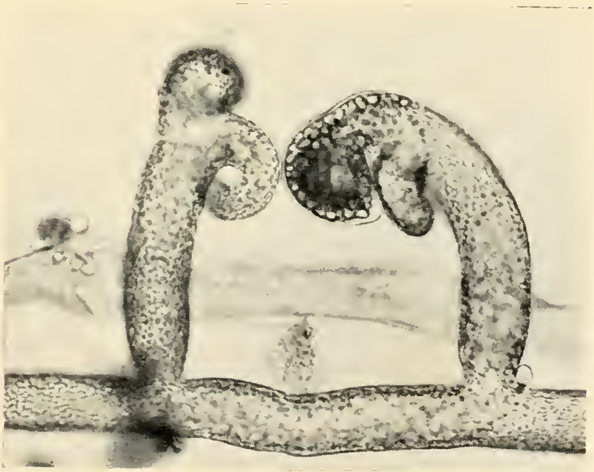

Fig. 81.—*Vaucheria sp.* Reproductive branches with lateral antheridia and terminal oogonia.

After fertilization a membrane develops across the oogonial aperture, and subsequently a thick, several-layered envelope is formed around the zygote, thus producing an **oospore.** At the same time the oil globules unite to form one or more large central globules, and the zygote enters a resting period of several months before germination. It germinates directly to produce a new filament without the intervention of zoospores (Fig. 82).

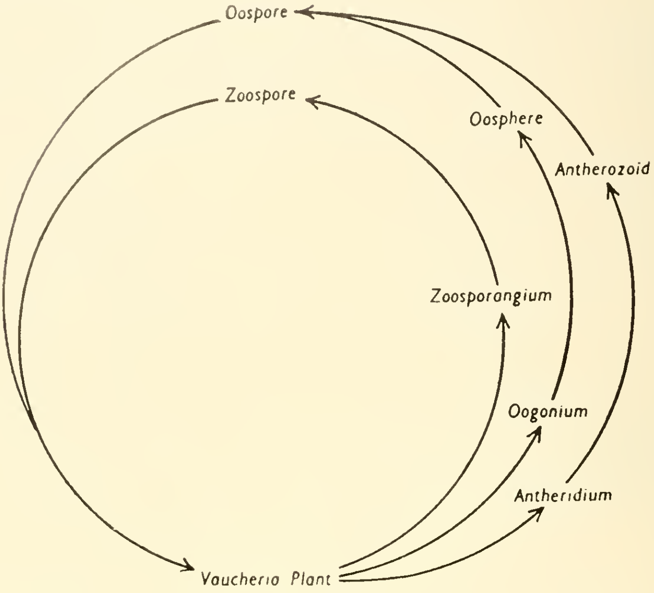

FIG. 82.—Life-cycle of *Vaucheria.*

Siphonocladiales

The Siphonocladiales are Chlorophyceae in which each branch of the thallus is composed of one or more coenocytes. Though in the simpler members the thallus consists of a single coenocyte and therefore may be comparable with that of the Siphonales, the group as a whole shows a progressive complexity, brought about partly by the development of septa which cut the large coenocytes into smaller ones and partly by the development of the branching system.

Asexual reproduction is by means of zoosporangia in which are developed zoospores, or by aplanospores. Sexual reproduction is by the fusion of isogametes.

Most of the species are marine and are more characteristic of the warmer temperate and tropical seas than of this country. Many are found in the Mediterranean while others occur particularly in the West Indies. A few genera are found in fresh water. A number of species are calcified, fossil types of which have been described. (See Volume III.)

We shall consider only one type, *Cladophora*, which is among the more advanced members of the group. In fact recent classifications have tended to favour separating it as an independent order, the Cladophorales, while relegating all the other families to the Siphonales, from which they have most probably arisen.

Cladophora

Species of this genus occur characteristically both in fresh water and also in the sea, and a few species are epiphytic or even epizoic. The species are very numerous and difficult to separate (Fig. 83).

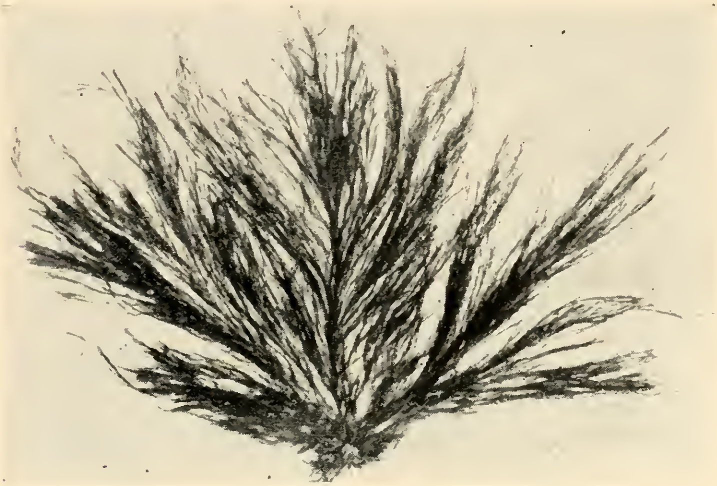

FIG. 83.—*Cladophora rupestris.* Form of entire plant.

The thallus is composed of branched, septate filaments formed of cylindrical coenocytes joined end to end. It is attached to the substratum by means of branched, septate rhizoids. Each branch grows by means of an apical segment. The separate coenocytes (Fig. 84) contain numerous nuclei which are either embedded in the meshes of the chloroplast or lie internal to it. The structure of the chloroplast is complex, and divergent views exist regarding its nature. It appears to consist of a parietal reticulum which lies in the cytoplasm, though additional chloroplast segments may develop inwards into the central vacuole. The meshes of this reticulum cover the longitudinal and transverse walls of the coenocyte and vary much in width. There are numerous pyrenoids scattered in it which can multiply by division. In unfavourable conditions the chlorophyll may contract

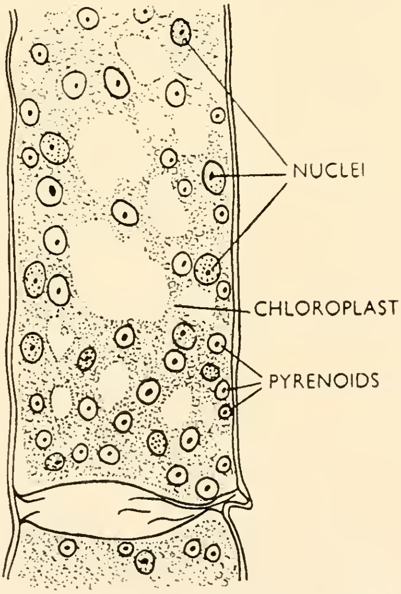

FIG. 84.—*Cladophora glomerata.* Young coenocyte in the autumn condition, the pyrenoids containing starch. (*After Carter.*)

around the pyrenoids in more or less spherical masses, thus giving the impression of separate discoid chloroplasts, which may explain the view expressed by some workers that the chloroplast is not a single reticulate structure but a number of small connected, discoid bodies. Fragmentation of the chloroplast has been observed not infrequently.

The wall of the coenocyte is composed of a series of thick, stratified membranes, which consist of an inner and an outer lamella, with a superficial pellicle which can be separated by treatment with acetic acid. Both lamellae show stratification which usually runs obliquely to the long axis of the coenocyte. There is little or no mucilage, which probably explains the great abundance of epiphytes which normally occur on the plants.

Branches usually arise at the upper end of a coenocyte and at first form a wide angle with the parent branch, for the septum cutting off the branch is developed nearly perpendicular to it. Sometimes two branches arise together, one on either side of the main axis.

Growth is by means of the apical segment, which, after elongating sufficiently, forms a transverse septum cutting off the greater part of the segment. At the beginning of such a division the protoplast is withdrawn from the region where the new septum will develop, the space so left being apparently filled with mucilaginous material. An annular bar of thickening is laid down here, extending transversely all round the cell. This forms the beginning of the cross wall which then gradually extends inwards towards the centre. At the same time it extends into and fuses with the inner lamella of the longitudinal wall. The formation of septa is in no way related to nuclear division.

The attaching organs consist of a number of septate, rhizoidal branches. These may sometimes spread out as stolons which either give rise to new upright filaments or their tips may grow out into a number of short cells, which later fall apart and serve as a method of propagation. The short cells formed on the rhizoids have thick walls and are abundantly supplied with food reserves. After separation they may undergo further wall thickening and function as over-wintering organs. Many species are, however, free-floating, as can be seen in the floating tangles (" flannel weed ") which are so characteristic of ponds. In the free-floating species smaller or larger parts of the vegetative branches may separate, develop thick walls, and being well supplied with food reserves may function, in some species, as the only means of reproduction.

Asexual Reproduction

Every coenocyte of a branch is potentially capable of functioning as a zoosporangium (Fig. 85), and it is by no means unusual to find all the cells producing zoospores at the same time. Prior to the formation of zoospores the chloroplast fragments and a gradual cleavage of the contents occurs in the cell. Meanwhile the wall of the zoosporangium may begin to swell at one side near its upper end. As this area continues to swell a rupture appears at its centre. Through this the zoospores finally escape.

The zoospores are small pyriform bodies with a small anterior beak and two apical flagella, or in some species four. These flagella are differentiated before the emergence of the spores. There are two granules at the point where the flagella are inserted and the chloroplast appears as a ring in the posterior part of the cell and shows a slow streaming movement. Those zoospores nearest the orifice escape first, squeezing their way through the opening with their flagella behind them, and they are followed by a steady stream of others. After about twenty minutes they settle down by their

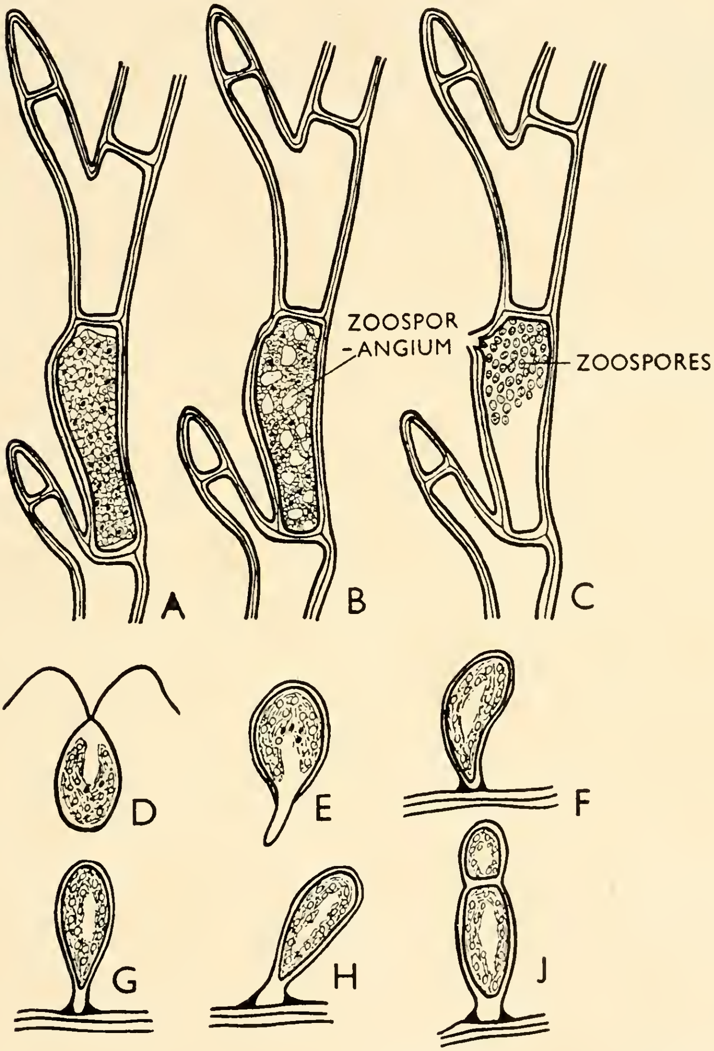

FIG. 85.—*Cladophora crispata.* Asexual reproduction. A to C, Formation of zoosporangium and liberation of zoospores. D, Motile zoospore. E to J, Attachment and germination of zoospore. (*After Cook.*)

anterior ends and elongate. A septum appears and gradually the coenocyte structure of the thallus is re-established.

SEXUAL REPRODUCTION

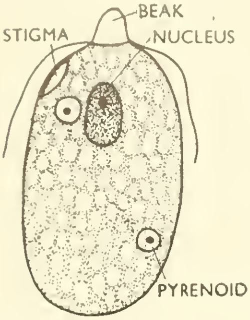

FIG. 86.—*Cladophora sp.* Mature gamete. (*From Fritsch.*)

The formation of gametes occurs in most species and probably in all. In some species it has been definitely established that the thallii are dioecious. Any segment of the thallus is potentially capable of functioning as a gametangium, and its development is similar to that of the zoosporangium. The gametes are isogamous and differ in no marked way from the zoospores, except that they are invariably biflagellate. They are liberated in a similar manner to the zoospores, and fuse externally to give rise to a zygote which germinates immediately to form a fresh *Cladophora* filament (Fig. 86).

ALTERNATION OF GENERATIONS

It has now been definitely established that in almost all species there is a strict alternation of sexual and asexual generations. These generations are morphologically alike. Meiosis occurs prior to the formation of the zoospores which therefore give rise to male and female monoploid plants, the diploid phase being established after gametic fusion, resulting in the formation of a sporophytic plant, on which the zoospores are produced. A similar type of alternation has been found in a small number of related genera.

The life-cycle of *Cladophora* may therefore be represented by the following diagram :—

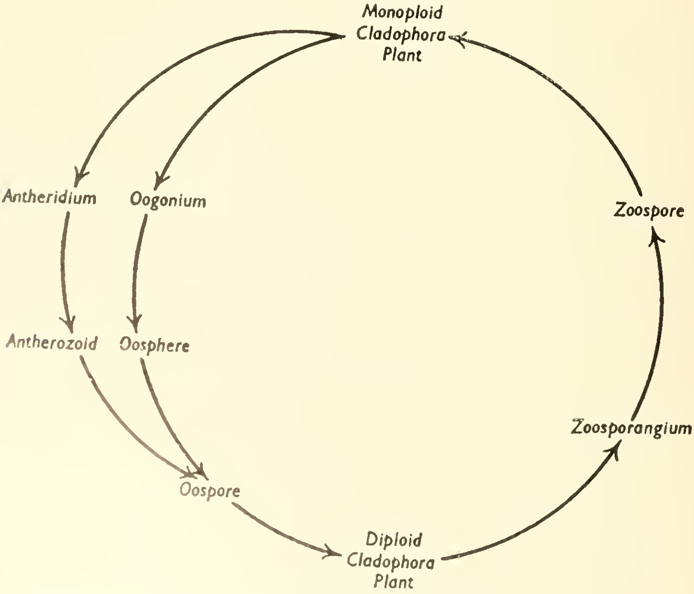

FIG. 87.—Life-cycle of *Cladophora*.

In *Cladophora glomerata* it has been shown recently that zoospore formation occurs at intervals all through the year, while gamete formation happens only in the spring and at the end of a long series of zoospore discharges. Gametes and zoospores are developed in distinct plants, but there is no reduction division in the formation of the zoospores. It appears that this species can produce a succession of diploid zoospore generations, after which meiosis occurs during the formation of the gametes. Conjugation restores the diploid condition. This condition resembles that which has been described in some members of the Siphonales.

CYANOPHYCEAE (Myxophyceae)

The Cyanophyceae are Algae in which the thallus may be either unicellular or filamentous. It is always enclosed in a gelatinous sheath. The cells possess **phycocyanin** (blue) and **carotin** (orange) in addition to chlorophyll, and the varying proportions of these pigments not only mask the green colour but cause a wide variation of tint from almost pure blue to brown. They occur chiefly in fresh water and on damp surfaces ; some are found in the soil, whilst a minority are marine. They constitute the principal vegetation of hot springs, some being able to live in water as high as 85° C.

Apart from their interest as the simplest of the Algae they are remarkable for their cytological structure. The cell wali is usually very thin and is composed either of pure cellulose or a hemi-cellulose. External to the wall is the gelatinous sheath, composed of pectic compounds.* It is sometimes thin and tough, sometimes massive and diffuse. It may also consist of multiple lamellae, and not infrequently forms a common investment round a group of filaments, or **trichomes** as they are called in this family. These sheaths may become very tough, and it is undoubtedly due to them that the plants can withstand high temperatures and considerable desiccation.

The protoplast is remarkably simple. It is more or less uniform, without any vacuole or plastids. The central region is almost colourless, and scattered in it are chromatin granules which represent all there is of a nucleus. These granules can divide, and they separate into two groups prior to cell division, but in some instances there appears to be little, if any, co-ordination between the grouping of these granules and the division of the cells. There is certainly no regular mitosis. In the external zone of the protoplasm the pigments are diffused throughout its substance and there are also present numerous minute granules, including oil drops, glycogen and others which are probably volutin and are called **metachromatic granules.**

Many of the filamentous species develop either terminal or intercalary **heterocysts,** which are easily recognized by their larger size, thick wall and homogeneous contents. The function of these bodies is not known.

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* A symbiosis with Nitrogen-fixing Bacteria, living on this sheath appears to be common among the Cyanophyceae.

Reproduction may take place by the breaking of the trichome, within the sheath, into short filaments of cells which are termed **hormogones.** The points of disjunction are marked by collapsed biconcave cells. The hormogones are set free by a breakdown of the sheath at the end of the parent filament. They are capable of slow movement though they have no flagella, and finally settle down and form fresh filaments. In one or two species reproduction may be effected by **gonidia,** which are tiny non-motile cells derived by the division of one or more cells of the parent plant. These are liberated and finally grow into fresh filaments. **Resting spores** may also be produced. These bodies arise from vegetative cells which increase in size, become gorged with reserve material, and are often yellow or brown in colour. They are frequently developed in association with heterocysts. The unicellular species generally multiply only by simple cell division.

Many species of the Cyanophyceae are world-wide in distribution. They are among the first organisms to colonize new ground and they were the first organisms found on the island of Krakatau after the eruption of 1883. They are found in the Arctic, even though they may be covered for months on end with snow and ice. On the other hand, as we have seen, they occur very commonly in hot springs. Some species live within the tissues or even within the cells of higher plants. Species of *Anabaena* are found in cavities in the fronds of the water-fern *Azolla*, and also in the roots of the gymnosperm *Cycas*. Species of *Nostoc* form colonies in the underground stem of the giant angiospermic marsh plant *Gunnera manicata* (Fig. 88). Many

FIG. 88.—*Gunnera manicata*. Transverse section of the underground stem showing colonies of *Nostoc* embedded in the tissues.

as we shall see later, are concerned in the formation of Lichens. Their wide distribution, coupled with their peculiar structure, seems to indicate that they are probably the most ancient and primitive of the Algae.

The Cyanophyceae are divided into several orders of which we shall consider only the Hormogonales, which includes most of the filamentous types.

Hormogonales

The Hormogonales are Cyanophyceae in which the filaments have no individual membrane on the vegetative cells. The trichomes are simple, free and sometimes coiled. They are septate, but the septa are frequently obscure. The cells are very uniform, short and discoid or rectangular in shape, with a uniform granular cytoplasm, divisible into two regions, a peripheral one containing the pigment together with glycogen and oil-drops, and a central region which is colourless and contains metachromatic granules. The trichomes may be free-floating, or may form a more or less mucilaginous mass on solid surfaces. **Heterocysts** occur only in certain families.

Reproduction is by means of **hormogones**, short lengths cut off from the parent filament which are capable of growing into mature trichomes. Thick-walled resting spores or **akinetes** are often developed, usually next to the heterocysts. No method of sexual reproduction occurs.

We shall consider one common type—*Nostoc*.

Nostoc

There are a number of common species which occur either terrestrially or as aquatics in mucilaginous masses (" moon-spit "), living either attached to a substratum or free floating. Each mass is composed of a more or less firm jelly or mucilage, with a denser surface layer, inside which are numerous twisted trichomes, which are yellowish-green in colour. These gelatinous masses may be either solid or hollow and as much as several centimetres in diameter ; they frequently break open to form flattened expanses with lacerated margins.

The **trichomes** are much contorted and form an intricately woven mass which is more crowded towards the exterior (Fig. 89). Each is composed of nearly spherical cells which are only loosely joined together. The **heterocysts** are intercalary and solitary, and are oval in shape and slightly larger than the vegetative cells (Figs. 90 and 91).

Reproduction

Hormogone formation is very common and results from the rupture of the trichome at points where a vegetative cell and a heterocyst join. The large numbers of trichomes in a colony is probably due to the development of the hormogones into fresh trichomes without being liberated from the colony.

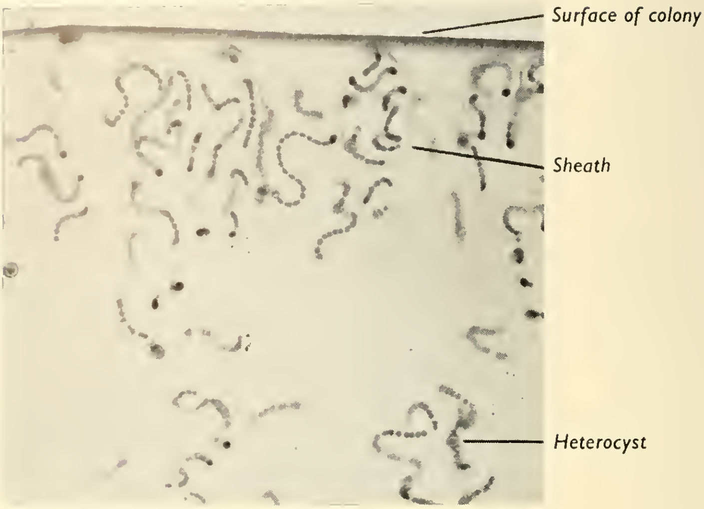

FIG. 89.—*Nostoc sp.* Section through part of a gelatinous colony showing embedded filaments with heterocysts. Each filament has an individual sheath of denser mucilage.

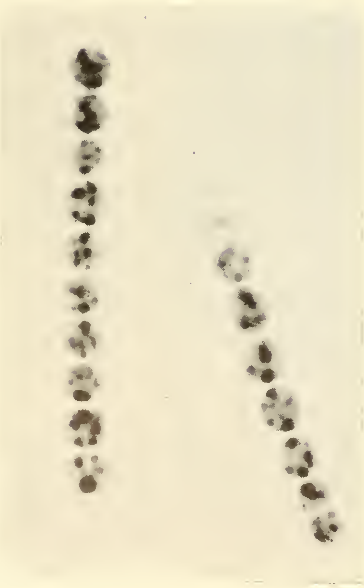

FIG. 90.—*Anabaena sp.* Cells stained with Methylene Blue showing metachromatic granules.

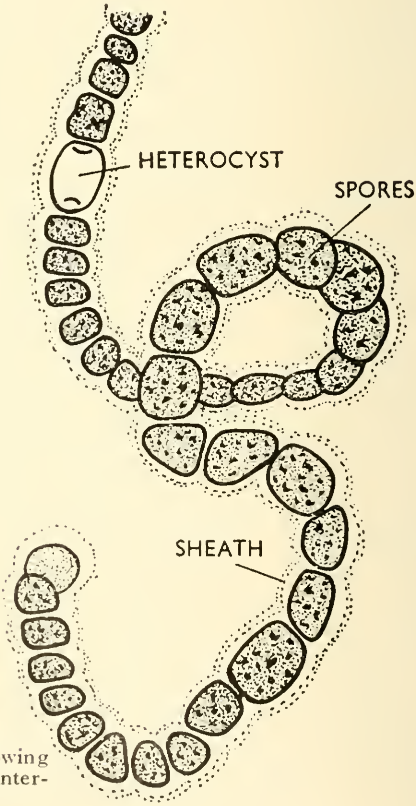

FIG. 91.—*Nostoc linckia.* Filament showing outer sheath, enlarged spores and intercalary heterocyst. (*After Pascher.*)

When the colony is mature **akinetes** may be formed from any or all of the vegetative cells, and it is not unusual to find all the cells between two heterocysts converted into akinetes. Each germinates to form a new trichome.

While many species grow on bare soil among mosses, others are subterranean, and have been found as much as three feet deep in the soil. Many are aquatic and live free-floating, attached to vegetation or on the bottom of the pond. A few species favour running water, particularly fast-flowing mountain streams.

Nostoc frequently forms the algal component of Lichens (*e.g.*, *Peltigera canina*, see p. 369), while one species is found in symbiotic association with *Anthoceros* (see p. 409).

CHAPTER V

THE ALGAE: PHAEOPHYCEAE, BACILLARIOPHYCEAE AND RHODOPHYCEAE

PHAEOPHYCEAE

THE Phaeophyceae are Algae in which an additional pigment, **fucoxanthin,** is developed, more or less completely masking the chlorophyll which is also present in the cells. Unicellular types occur, and there are a number of genera in which the majority of the species are filamentous, but the bulk of the species included in this group have a more complex thallus built up of either cellular tissue or of a number of central filaments bound together by mucilage, each of which gives off lateral branches in such numbers that they form a tissue surrounding the central filaments. In such types the central filaments are termed the **medulla,** while the surrounding tissue is spoken of as the **cortex.** In the most advanced types the cells of the medulla become modified into specialized conducting elements, which assist in the transference of the food material from one part of the plant to another. We find, then, in the higher Phaeophyceae much greater morphological differentiation than is met with in the Chlorophyceae.

Sexual reproduction by means of isogametes is the method most common among the lower orders, while in the higher orders reproduction may be either isogamous or oogamous. Asexual reproduction is by means of zoospores, which differ from those of the Chlorophyceae in being pear-shaped with two laterally placed flagella.

Many of the Phaeophyceae exhibit **alternation of generations,** that is to say, there is a definite and immutable alternation of sexual and asexual individuals. The zygote develops into a plant which may or may not resemble the parent and on which only asexual reproductive bodies are borne. These on germination produce a plant, not necessarily like its parent, but like the " grandparent," on which sexual reproductive bodies are developed. The plant which produces the gametes is termed the **gametophyte,** and that which develops the asexual spores is called the **sporophyte.** In alternation of generations therefore there is an alternation of gametophyte and sporophyte generations. This obligatory alternation of generations is extremely important, and although the Phaeophyceae are the first group in which we meet it as a general characteristic, we shall find that in all higher plants it invariably occurs, though it may not be easy to recognize it at first sight, owing to secondary modifications which have taken place in the course of evolution.

The Phaeophyceae are divided into a number of orders of which we shall consider examples from five :—

1. **Ectocarpales** (*e.g.*, *Ectocarpus*).
2. **Cutleriales** (*e.g.*, *Cutleria*).
3. **Dictyotales** (*e.g.*, *Dictyota*).
4. **Laminariales** (*e.g.*, *Laminaria*).
5. **Fucales** (*e.g.*, *Fucus*).

Ectocarpales

The Ectocarpales are a small group of relatively simple Phaeophyceae in which the thallus is filamentous in its fundamental structure, though very varied in form. In the simplest cases the filaments are entirely free, but in some other forms the lower parts of the filaments are variously aggregated together to form more or less solid bodies, the ends alone remaining free.

The vegetative cells in Ectocarpales are shortly cylindrical, containing irregularly shaped **chromoplasts** with **pyrenoids.** There is no special apical cell. Growth takes place by the division of an intermediate group of cells in the filament, which form a **meristematic zone.** Such a method of growth, which is neither apical nor basal, is called **intercalary.**

There are two characteristic reproductive structures. Firstly, **unilocular sporangia,** which consist of single enlarged cells, the contents of which divide up, without the formation of any cell walls, to liberate a large number of motile cells which are pear-shaped and have two flagella, one directed forwards and the other backwards. Secondly, **gametangia** (plurilocular sporangia), derived from the cells of a short side branch. These divide up by transverse and longitudinal walls into a large number of small cubical cells, each of which produces a biflagellated motile **gamete,** similar in structure to the products of the unilocular sporangia.

Meiosis takes place at the first nuclear division in the unilocular sporangium, so that the spores from this type are definitely monoploid. In general, they function as asexual **zoospores,** giving rise to haploid plants. The plurilocular sporangia, on the other hand, are generally regarded as gametangia, the cells from which fuse in pairs, and from the zygote thus formed diploid plants arise. Variations of this behaviour are, however, known, as explained below.

We shall consider only one example of this order, *Ectocarpus*, but as there is considerable variation in details between species, the description must necessarily be a general one.

Ectocarpus

Species of the genus *Ectocarpus* are very common in sea water around the British coast. Some are attached to rocks and stones, but many grow attached to other Algae, and are therefore said to live as **epiphytes.** We must distinguish between an epiphyte, in which the plant obtains no nourishment from the organism on which it lives, and a **parasite** in which the reverse is the case ; for the parasites live at the expense of the second plant, which is then termed the **host plant.**

The thallus of *Ectocarpus* is generally filamentous and repeatedly branched (Fig. 92). It is made up of two parts, a creeping portion which covers the substratum and serves as the **holdfast,** and a number of upright branches which arise from it. These upright branches generally consist of a single row of cells, though in some species longitudinal cell divisions occur. The cells are small and rectangular, each containing a single nucleus and a number of small spherical bodies containing the brown pigment, which are called **chromatophores** or **chromoplasts. Pyrenoids** are present in the chromoplasts. This is interesting because these bodies, which are characteristic of the Chlorophyceae, are only found in the most primitive members of the Red and Brown Algae.

Growth takes place by the division of a series of small cells situated near the base of the vertical branches. These cells are generally small and continue throughout the life of the branch to cut off additional cells from their upper surfaces. The cells of the more apical part of the branch do not divide and are more elongated than those of the actively dividing or **meristematic** region. This is therefore an example of **intercalary growth** (Fig. 93).

FIG. 92.—*Ectocarpus sp.* Form of plant bearing zoosporangia.

ASEXUAL REPRODUCTION

The asexual reproductive organs consist of **unilocular zoosporangia** which are developed on the side branches (Fig. 94). They originate as simple globular or pear-shaped cells which become densely filled with protoplasm. The original nucleus divides first meiotically and then repeatedly by mitosis. Around each daughter nucleus a small quantity of protoplasm collects to form a **zoospore.** It consists of a small, rather elongated cell, and contains besides the nucleus a single brown plastid. Two flagella are developed at one side of the zoospore, one pointing forwards and the other backwards. On liberation the zoospore swims away, eventually settles down and grows into a monoploid plant.

Sexual Reproduction

The sex organs are borne on monoploid plants and consist of **gametangia** (Fig. 95), which develop laterally, either sessile on a branch or at the end of a short row of sterile cells.* Each gametangium is composed of a number of chambers, separated from one another by transverse and longitudinal walls. In each of these compartments one, or sometimes two, gametes are formed.

They do not differ morphologically from the asexual zoospores, but on liberation they fuse in pairs. In some species, *e.g.*, *E. secundus*, there is a difference in the size of the gametes, and in such cases it is seen that the smaller ones cluster around the larger ones. It is concluded that the larger represent the female gametes, while the smaller are regarded as the males. After conjugation the zygote develops into a diploid plant, which eventually produces sporangia.

Sexual plants are as a rule dioecious, gametes from one plant behaving for the most part consistently either as males or as females. There are, however, exceptions, cases of irregular behaviour, which led Hartmann to the doctrine of **relative sexuality,** which regards sex as a quantitative character, which may be either strong or weak, so that a given cell may behave as either male or female according to the strength of sex in the cell with which it pairs.

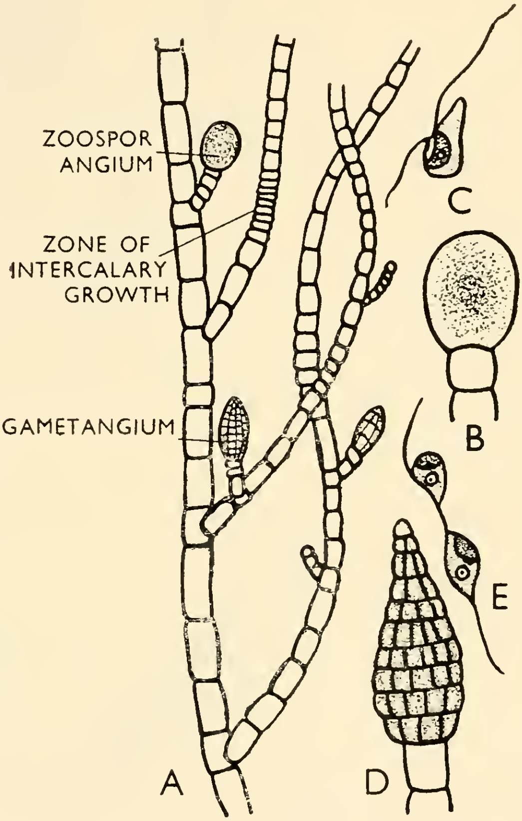

Fig. 93.—*Ectocarpus sp.* A, Branching filaments showing intercalary growth and reproductive organs. B, Young zoosporangium. C, Zoospore. D, Gametangium. E, Conjugation of gametes.

As mentioned above under the heading of Ectocarpales, certain variations in the life history of *Ectocarpus* exist, which have given rise to considerable controversy in regard to its methods of reproduction. The principal point to be noticed is that both monoploid and diploid plants occur, which are morphologically indistinguishable. There is evidence that in some species they may be geographically separated. Monoploid plants appear to form

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* In *Pylaiella*, a very common and closely related Alga, the gametangia are intercalary.

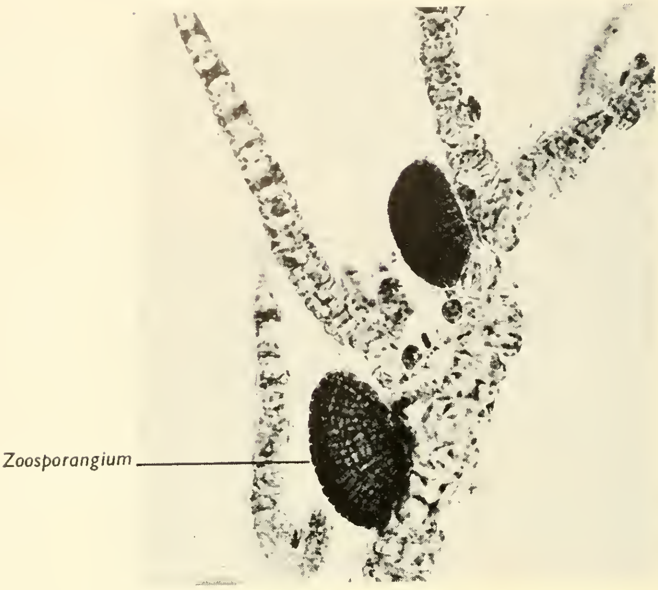

FIG. 94.—*Ectocarpus sp.* Branch with zoosporangium containing zoospores.

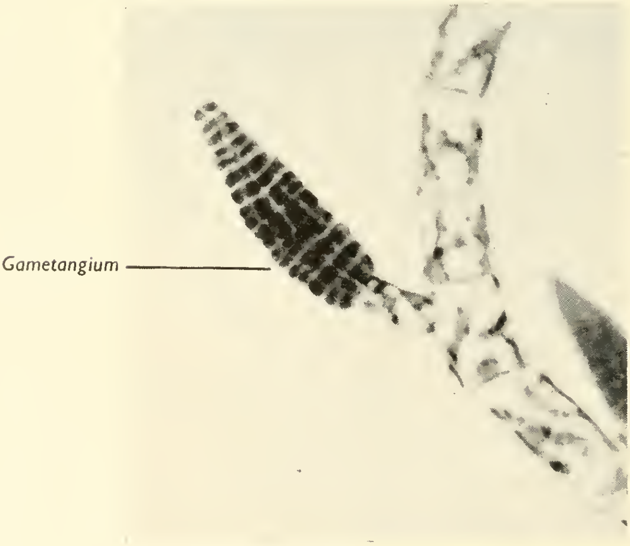

FIG. 95.—*Ectocarpus sp.* Branch with gametangium.

only gametangia, which produce gametes that fuse in pairs. They may therefore be considered as true gametophytes. Diploid plants, on the other hand, may produce both gametangia and zoosporangia (Fig. 96). In this case the products of the gametangia are diploid and germinate without conjugation like zoospores. The products of the unilocular sporangia are, however, monoploid. Most observers agree that they too germinate without fusion and regard them as true zoospores. It has been claimed, however, that they may fuse in pairs, producing diploid plants, but the actual development of such apparent conjugations has never been observed. If it occurs we have here a complete inversion of the normal reproductive order.

The occurrence of conjugation between the motile cells produced in sporangia has been interpreted as implying, in these cases, the complete suppression of the gametophyte stage, the products of the sporangia behaving directly as gametes instead of germinating to produce another vegetative generation. This special case in *Ectocarpus* would therefore be comparable to that in the normal life-history of *Fucus* (Fig. 96).

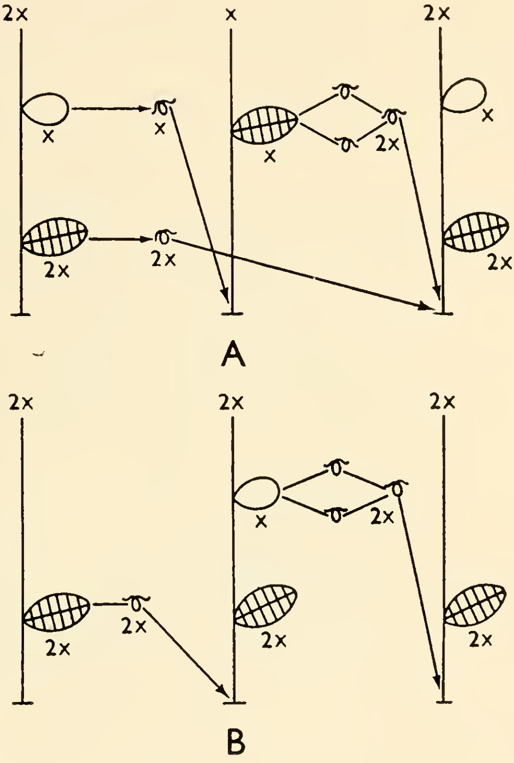

Fig. 96.—*Ectocarpus*. Variations of the life-history. A, Diplobiontic type with both diploid and monoploid plants. Gametangia produce diploid swarmers which germinate without conjugation. B, Haplobiontic type. All plants are diploid. The zoosporangia produce monoploid swarmers which conjugate in pairs.

Cutleriales

The Cutleriales are Phaeophyceae in which there is an alternation of generations between a large upright gametophyte and a small prostrate sporophyte. The gametangia are borne on short filaments arising from the surface layer of separate gametophyte plants, and the number of gamete cells produced in the male gametangium is considerably greater than those in the female. It is only on the structure of the sex organs that the sexes can be distinguished. The asexual plants give rise to zoosporangia, from which a number of zoospores are liberated. Growth of the thallus is peculiar. The apices of the branches are composed of clusters of uniseriate filaments. These filaments coalesce below to form a solid tissue. At or near the base of each filament is a zone of actively dividing cells, which cut off above more cells to the filaments, while at the same time contributing below to the solid tissue of the thallus. Such a type of intercalary growth is sometimes referred to as **trichothallic.**

Only one family, the Cutleriaceæ, is included in this order, and it contains only two well-known genera of which we shall consider one, *Cutleria.*

Cutleria multifida

This Brown Alga occurs somewhat rarely around the British coasts below low-tide mark, and, though apparently widely distributed, the plants are usually found isolated. The male and female plants vary with the locality, so that it is difficult to find any feature whereby the sexes can be distinguished clearly from one another.

These plants are attached to the rock on which they grow by a small holdfast (Fig. 97). The thallus is thin and irregularly branched, the branches varying much in width and frequency. Each branch terminates in a collection of filaments of cells of varying length (Fig. 98), as described above. In section the thallus is seen to be composed of large central parenchymatous cells surrounded by several layers of much smaller cells, which contain the pigments and form the assimilatory tissue of the plant. In addition to the terminal filaments or hairs, tufts of similar hairs may be developed upon the whole surface of the thallus.

FIG. 97.—*Cutleria multifida.* Form of the entire sexual plant.

THE MALE GAMETANGIUM

The male gametangia occur over the whole surface of the plant either in small or large clusters (Fig. 99), usually in association with the hairs. Both the hairs and the gametangia arise from superficial cells of the thallus. The cell grows out and divides to give a stalk-cell below and the gametangium above. Further divisions of the stalk-cell may occur so that a filament is produced. In this case not only does the terminal cell become a gametangium but one or more of the cells of the filament may produce lateral branches terminating in gametangia.

Fig. 98.—*Cutleria multifida.* Apex of a branch of the thallus showing trichothallic growth.

Fig. 99.—*Cutleria multifida.* Section of thallus showing a cluster of male gametangia on branched stalks.

Inside the gametangium the nucleus divides and two cells are formed separated by a wall ; more divisions follow, until the greatly enlarged gametangium consists of a number of parallel rows, each containing twenty-four or more cells. Each of these cells finally becomes a male gamete mother cell. Each cell has a single nucleus and associated with it a red pigmented eye spot. When mature a portion of the wall of the mother cell dissolves, leaving a small pore through which the gamete is discharged. In this process the flagella emerge first and show active movement, while the contents of the cell are still emerging.

The Female Gametangium

Like the male, the female gametangia are scattered over the whole surface of the female plant and may be developed alone or associated with hairs (Fig. 100). These hairs may develop long before any evidence of the gametangia is seen. Both the hairs and the gametangia arise from superficial cells of the thallus, but usually the filaments are shorter and not so much branched as in the male. The development of the gametangium is similar to that of the male, but the number of mother cells produced is considerably smaller. A mature female gametangium consists of from four to seven tiers, each being composed of from four to eight cells. Thus from sixteen to about fifty-six female gametes are ultimately liberated from each gametangium.

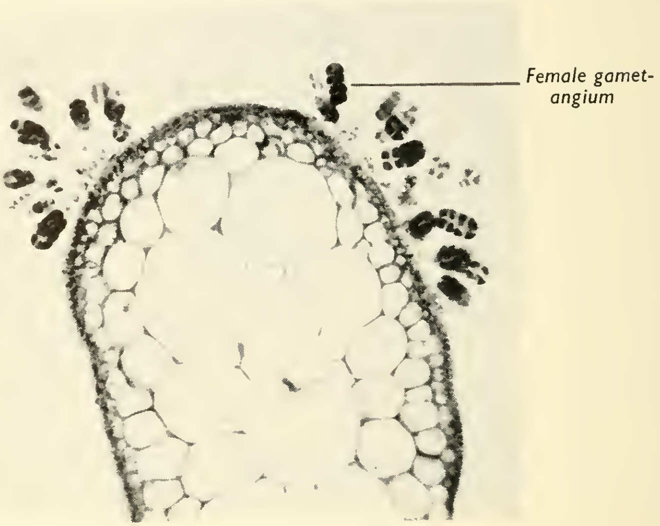

Fig. 100.—*Cutleria multifida.* Transverse section showing structure of thallus and two clusters of female gametangia.

The mature female gamete is an oval structure with two long flagella, the longer one pointing forward and the other backwards, attached to its side in the region of a red pigment eye spot. The gamete also contains about thirty oval plastids. When first liberated it is actively motile but it soon becomes sluggish, the shape becomes spherical and the flagella are withdrawn.

FERTILIZATION

Both kinds of gametes are discharged at any time of the day or night, though it has been found in the Mediterranean that they are most abundant between 5 and 7 A.M.

The male gamete is considerably smaller than the female (Fig. 101); it possesses two unequal flagella like those of the female, and a red pigment spot, but few or no plastids. It may remain active for as long as twenty hours. The active male gamete usually becomes attached to a female gamete only when the latter has become sluggish, but before it has produced any enveloping wall. The flagella of the male gamete are then withdrawn, and the cytoplasms of the two cells coalesce and fusion of the two nuclei follows.

Should a female gamete fail to be fertilized it is still capable of growth, though only after becoming enclosed in a cell wall. A period of rest usually follows before any division takes place.

Compared with the rate of cell division in the fertilized zygote the rate of development of these apogamous sporelings is very slow.

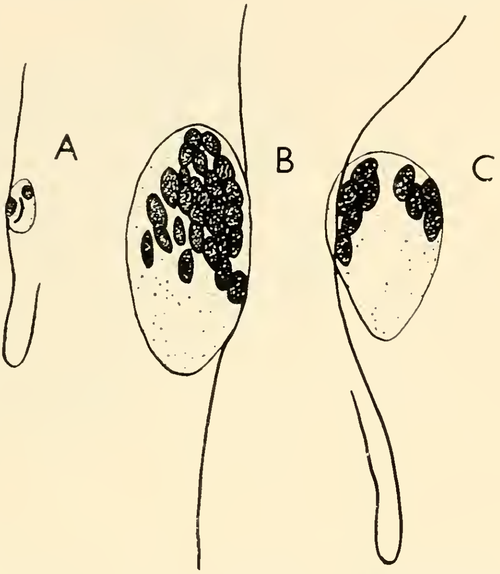

FIG. 101.—*Cutleria multifida.* A, Male gamete. B, Female gamete. C, Zoospore. (*After Yamanouchi.*)

DEVELOPMENT OF THE ZYGOTE

The development of the zygote and of the apogamous female gamete is similar. The cell first elongates, forming a spherical apex attached to a filamentous lower end. Division follows cutting off the spherical apex; repeated transverse divisions of the apical region follow, so that by the time the sporeling is about ten days old it consists of a columnar structure standing upright on the substratum with a stalk composed of one or two cells and a head made up of three or four cells. The direction of growth now changes and there is formed a flat plate of tissue derived from the basal end of the stalk. The basal expansion grows by division of the marginal cells, which causes zonation of growth to appear similar to that in *Coleochaete*. As growth continues the outline of this flat plate of cells becomes more and more irregular, and by the time it is about a month old it is large enough to be seen with the naked eye. Meanwhile the columnar tissue has ceased to grow, though the prostrate thallus continues to increase by marginal growth.

The Mature Sporophyte (*Aglaozonia reptans*)

For a long time the sporophyte of *Cutleria* was thought to be an independent seaweed and was known as *Aglaozonia reptans* (Fig. 102). It possesses a creeping habit, and grows on rocks and sea urchins' shells to which it becomes attached by means of rhizoids, developed from the superficial layer of its lower surface. It may reach a diameter of two or three inches (Fig. 103). It was not until 1898 that it was shown that *Aglaozonia reptans* was really the sporophyte of *Cutleria multifida*.

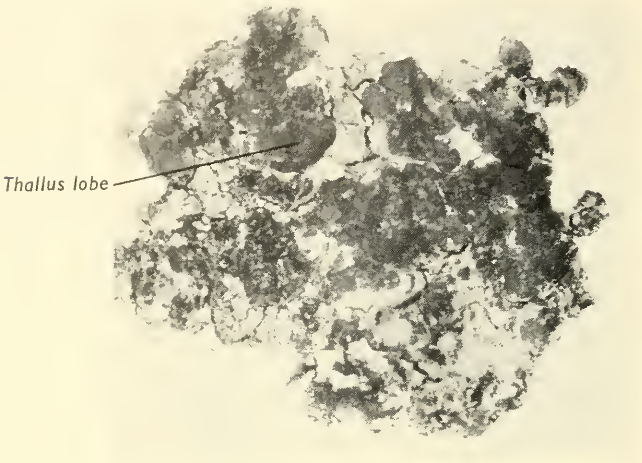

Fig. 102.—*Aglaozonia reptans.* Thalli growing attached to rock. Natural size.

A section through the thallus reveals one or two layers of small cells on the upper and lower surfaces, and in the middle two or three layers of very large parenchyma cells. From any superficial cell of the lower surface a rhizoidal holdfast may arise.

The Zoosporangium

The zoosporangia are produced on the upper surface of the thallus and are formed in patches, each composed of hundreds or thousands of zoosporangia, which are packed close together in a palisade arrangement (Fig. 104). Each zoosporangium arises from a superficial cell of the thallus, which elongates slightly and divides to give a small basal stalk cell and an upper cell, which becomes the zoosporangium. This latter cell enlarges and elongates until finally it is about three times as long as it is wide, with a somewhat swollen top. The nucleus of the zoosporangium now divides by reduction division, which is followed by further mitotic divisions, until from eight to thirty-two nuclei are formed. Cleavage furrows now appear in the cytoplasm, which divide the contents into zoospores. A pore develops at the top of the zoosporangium and through this the zoospores escape (Fig. 105).

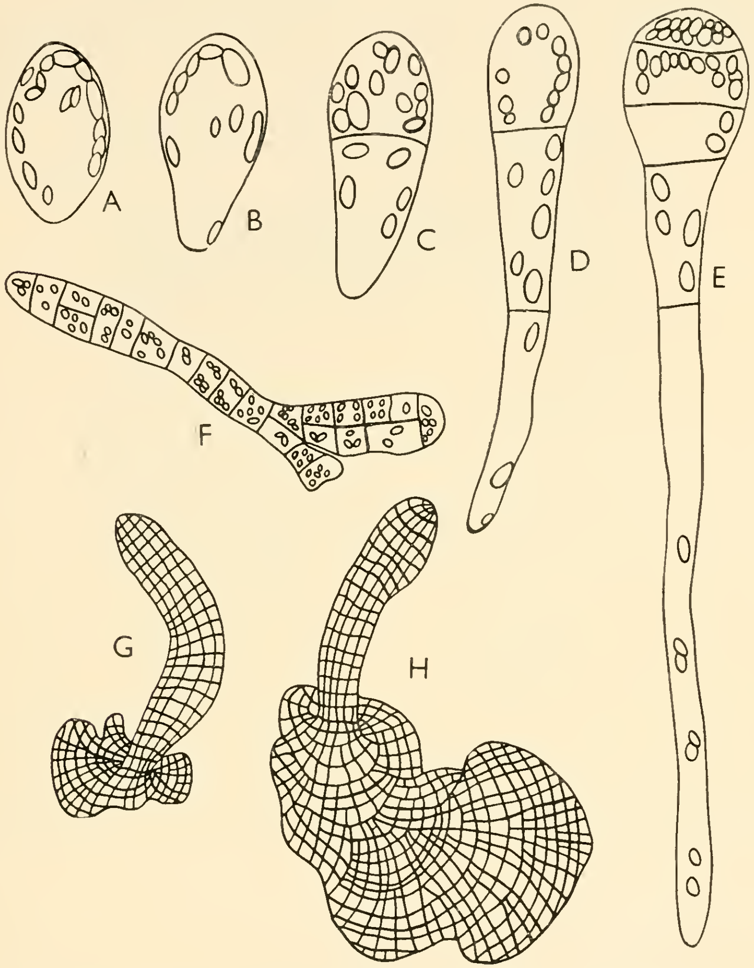

FIG. 103.—*Aglaozonia reptans.* A to E, Early stages in development of the *Cutleria* zygote. F, G and H, Older stages in development of the *Aglaozonia* thallus. (*After Yamanouchi.*)

THE GERMINATION OF THE ZOOSPORES

When liberated the zoospore is an oval body containing about twenty plastids, associated with which is a single red pigment spot. It possesses two lateral flagella of unequal length, one being about twice the length of the other. The longer one is directed forwards, while the shorter trails behind.

The zoospore may remain active for up to an hour and a half, after which it becomes sluggish, the flagella are withdrawn, the cell becomes spherical and a wall is laid down.

Division soon follows and a filament is formed. As growth continues the cells at the posterior end begin to divide longitudinally so that a widening of the filament occurs and it begins to assume a thalloid form, while rhizoids develop from the lower end (Fig. 106). Gradually this lower portion, developing by lateral growth, forms a funnel-shaped structure. From the margin of this structure delicate multicellular filaments grow out, which become the apical tufts of branches, and gradually the typical *Cutleria* plant becomes differentiated.

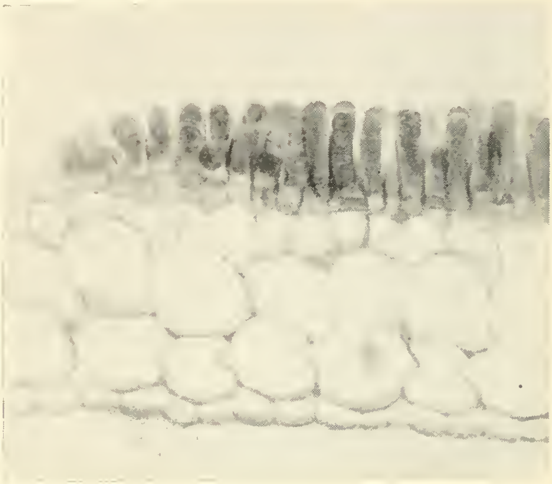

Fig. 104.—*Aglaozonia reptans.* Vertical section of thallus showing zoosporangia on upper surface.

Alternation of Generations

Cutleria shows an alternation of generations between a large gametophyte plant which is unisexual and a small sporophytic plant. In the development of its reproductive organs it is essentially comparable with *Ectocarpus*, though there is more differentiation both in the number and size of the two kinds of gametes. It may be therefore regarded as a specialized type derived from a form like *Ectocarpus*, in which the asexual plants have been reduced in size, while the gametophyte plants have become more complex, especially in their vegetative structure. In certain genera of the Ectocarpales we have examples in which longitudinal division of some of the cells of the filaments occur, and thus it is possible to see the way in which the thallus of *Cutleria* may have originated. The zoospores produced as a result of meiosis give rise to male and female plants, and it is reasonable to assume that as a result of genetic segregation these male and female plants should

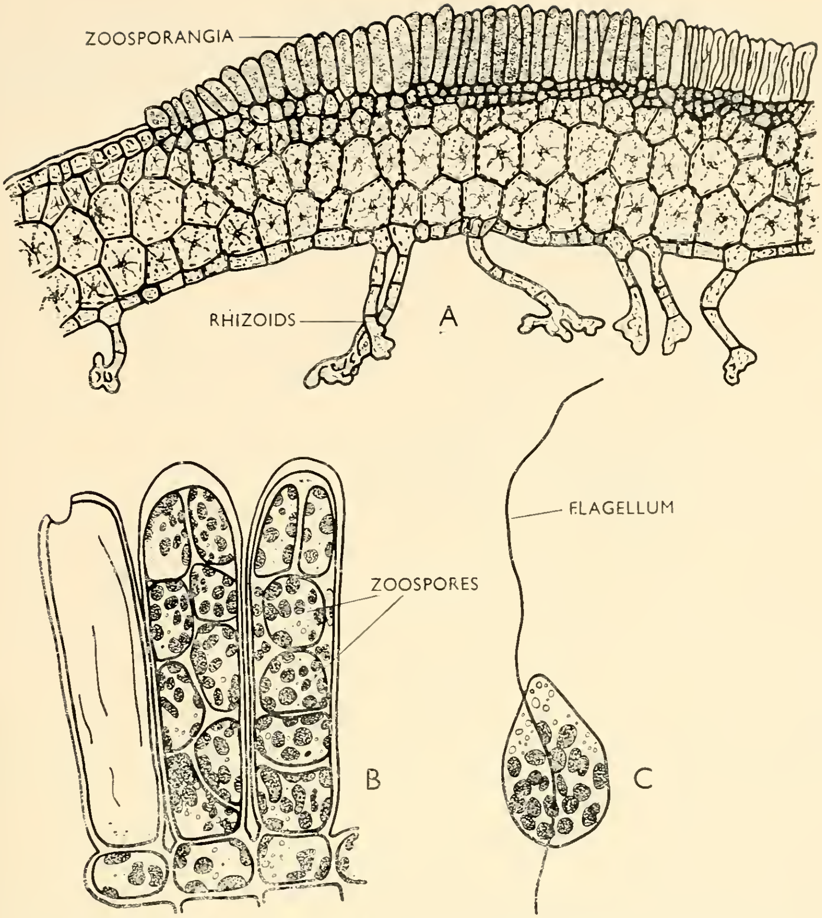

FIG. 105.—*Aglaozonia reptans.* A, Section of thallus showing zoosporangia. B, Enlarged zoosporangia containing zoospores. C, Zoospore. (*From Oltmanns.*)

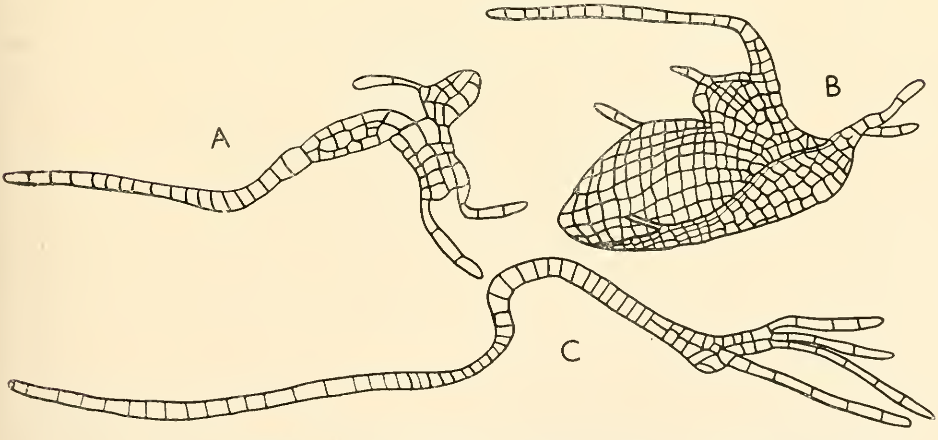

FIG. 106.—*Cutleria multifida.* A, Young stages in the development of the *Cutleria* thallus from the zoospore of *Aglaozonia.* B, Shows the formation of a funnel-shaped structure from the margins of which the branches develop. (*After Yamanouchi.*)

be produced in equal numbers. The *Aglaozonia* stage is comparable with the asexual stage of an *Ectocarpus*, and the early development of the zygote

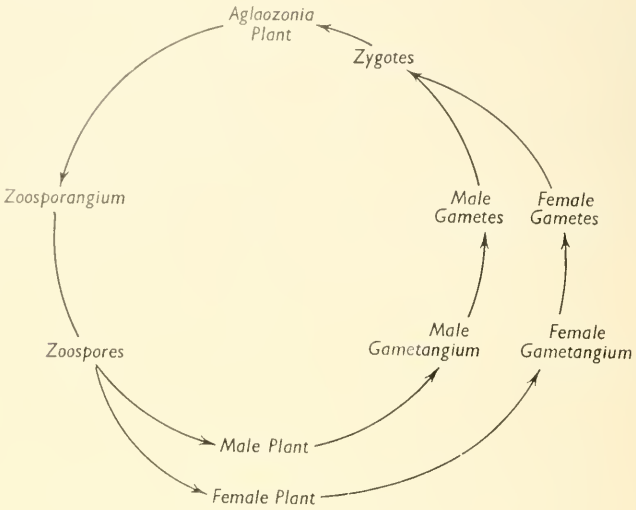

Fig. 107.—Life-cycle of *Cutleria*.

produces a filament comparable with an *Ectocarpus* plant. The flat thallus is a secondary development facilitating a greater production of zoosporangia (Fig. 107).

Dictyotales

These Algae are Phaeophyceae in which a definite alternation of generations occurs and in which the sporophytic and gametophytic plants are morphologically indistinguishable. Sexual reproduction is oogamous, while the organ of asexual reproduction is a non-motile spore termed a **tetraspore,** so called because only four spores are produced in each sporangium.

This is a small order with only a few genera, and we shall consider *Dictyota dichotoma* as our example.

Dictyota dichotoma

This Alga is common around the coast of Britain, growing in pools between tide-marks (Fig. 108). The strap-like thallus is 10 to 20 cm. long and consists of rectangular cells arranged in a single layer, with a superficial layer of smaller cells on each side of the thallus. Small tufts of hairs develop from scattered groups of these surface cells. The thallus is attached to the rock by a basal **holdfast.**

The thallus branches repeatedly, each division giving rise to two equal branches. Such a type of branching is termed **dichotomous.** Growth is by means of one large apical cell on each branch, which divides vertically into two equal halves when branching is about to take place. The male and female organs are borne on separate plants, and the asexual reproductive organs are produced on different plants from the sexual ones ; but, as far as

FIG. 108.—*Dictyota dichotoma.* Thallus of plant about half natural size.

their general appearance is concerned, all three kinds of plants are exactly the same.

ASEXUAL REPRODUCTION

The sporangium arises from a superficial cell of the thallus, which grows into a small spherical projection from the surface (Fig. 109). Its nucleus

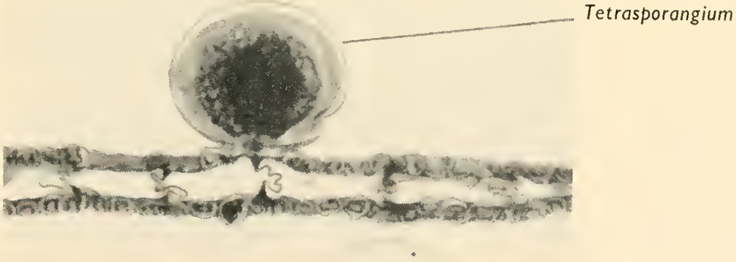

FIG. 109.—*Dictyota dichotoma.* Section of sporophytic thallus bearing a tetrasporangium.

enlarges and then divides meiotically, so that four monoploid nuclei are produced and the cytoplasm divides into four portions. No separating walls are formed, but the four monoploid spores are eventually liberated by a breakdown of the wall of the sporangium. These spores have no flagella.

The term **tetraspore,** which is applied to them, is used also for the asexual spores in the Rhodophyceae (see p. 158) which are also formed in fours, but the number is not constant in the Dictyotaceae, some genera producing eight in each sporangium. The **tetrasporangia** are, of course, equivalent to the sporangia of *Ectocarpus.*

On germination a tetraspore produces a fresh *Dictyota* plant, resembling in appearance the parent from which it was developed, but bearing gametes.

SEXUAL REPRODUCTION

The sex organs are antheridia and oogonia. They are arranged in groups or **sori** on the surface of the thallus on separate plants. Each **antheridium** arises from a superficial cell of the thallus (Fig. 110). This cuts off a lower stalk cell and an upper or antheridial cell which enlarges and divides, like a gametangium of *Ectocarpus*, into a large number of parts, so that, at maturity, some 1,500 antherozoids are liberated. As there are between 100 and 300 antheridia in each sorus, and as the number of sori on a full-grown plant may be well over 3,000, there is a fortnightly production of something like 500 million antherozoids from each mature plant, which means that there are on the average about 6,000 male gametes to each female. These antherozoids are pear-shaped and very small, and each is provided with two lateral flagella, the one which is directed backwards being much reduced in length. Each antheridial sorus is surrounded by two or three rings of sterile cells, called the **paraphyses.**

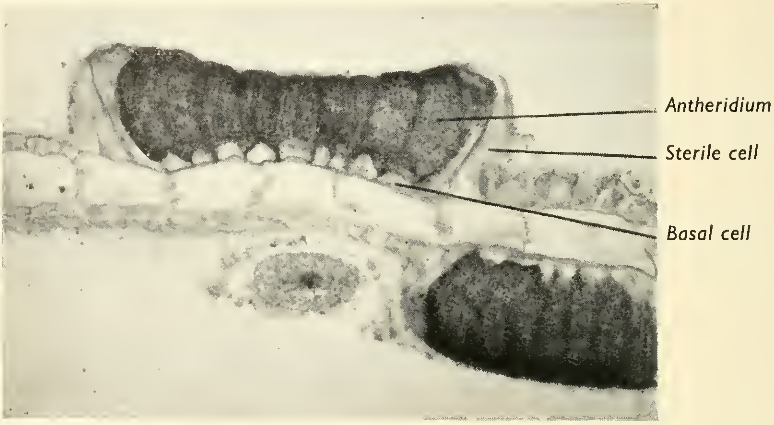

FIG. 110.—*Dictyota dichotoma.* Section of gametophytic thallus with sorus of antheridia. Note the sterile marginal cells.

The **oogonium** also develops from a superficial cell of the female thallus (Fig. 111). This cell divides into two, the lower forming a stalk cell, and the upper the oogonium. Inside the oogonium a single **oosphere** is formed, which is liberated as a naked mass of protoplasm by the breakdown of the oogonial wall. Each female sorus contains twenty-five to fifty oogonia which are not surrounded by paraphyses.

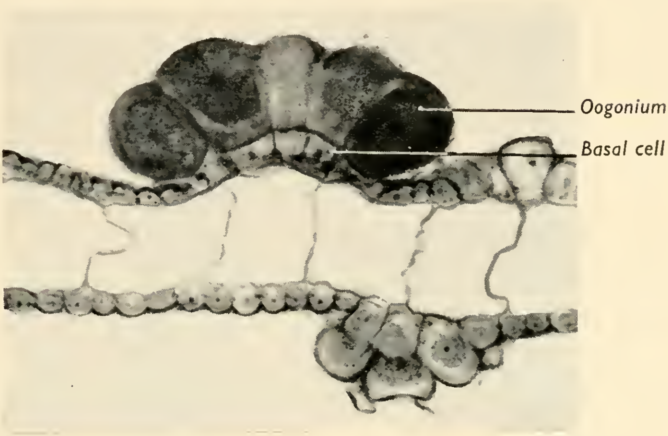

FIG. 111.—*Dictyota dichotoma.* Section of gametophytic thallus with sorus of oogonia.

Both kinds of gametes are set free in large quantities at intervals of fourteen days, shortly after the highest spring tides. This periodicity is hereditary and is maintained even under culture in aquaria. Fertilization occurs in the sea water and is effected by the movement of the antherozoids in large numbers to the oosphere, followed by the penetration of the oosphere by one of the antherozoids. Even if an oosphere fails to be fertilized it is capable of development to a limited extent.

Under normal circumstances the zygote germinates at once to produce

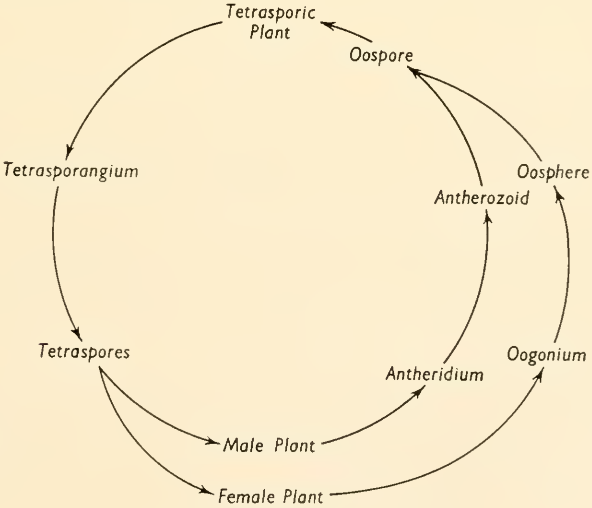

FIG. 112.—Life-cycle of *Dictyota.*

a fresh diploid plant, like the parents in appearance, but on which eventually tetrasporangia will be produced.

It will be seen, then, that *Dictyota* exhibits a typical alternation of generations between a diploid tetrasporic plant on the one hand, which is regarded as the sporophyte, and two haploid sexual plants, the male and the female, which constitute the gametophytes. The life-history of *Dictyota*, then, may be graphically represented by the diagram (Fig. 112).

Laminariales

The Laminariales are Phaeophyceae in which there is a marked alternation of dissimilar generations in which the sporophyte is large and conspicuous while the gametophyte is small and filamentous.

Although species of the Laminariales are widely distributed in temperate seas, the bulk of them occur in the colder waters of the North Pacific and North Atlantic oceans. Several species are common just below low-tide mark around the British coast.

The thallus is large, sometimes exceptionally so, for the order includes the largest of all the seaweeds, such as *Lessonia* and *Macrocystis* ; the latter reaches 200 ft. in length and grows at a depth of 60 to 100 ft. In other species, however, the thallus may be much smaller and more comparable with other brown seaweeds. The largest British species is *Saccorhiza bulbosa*, the " Sea Furbelows," which may grow up to 15 ft. in length.

The gametophyte is small and filamentous, and has only been studied critically in a few species. The sex organs are borne on separate plants and consist of antheridia and oogonia. The former liberate antherozoids, but the oosphere after fertilization remains within or attached to the oogonium. The sporophytic plant may be either annual or perennial.

We shall consider only one genus of this order—*Laminaria.*

Laminaria

There are a number of common British species, all of which agree in general structure and life history, but as they differ from one another very markedly in external form it will be desirable to outline briefly these differences at the outset so far as the common species are concerned.

Laminaria saccharina (Tangles) (Figs. 113 and 114).—In this species the thallus consists of an undivided frond with a wavy margin, arising from a rather short, thin, round stalk, which is attached by a rhizoidal holdfast. It is perennial, grows up to 6 ft. long and occurs from low-water mark to a depth of 10 fathoms.*

Laminaria digitata (Kelp) (Fig. 115).—In this species there is a smooth, thick stalk which widens out gradually into a broad frond which is divided palmately into a number of separate fingers. It is a considerably larger species than the last and the degree of dissection of the lamina varies considerably.

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* A fathom = 6 feet.

It may be up to 12 ft. long and is attached by an elaborate rhizoidal system. It occurs between low water and 15 fathoms.

Laminaria hyperborea (Tangles).—This species resembles *L. digitata* in the shape of the thallus, but differs from it in that the stipe is not smooth and it expands abruptly into the palmate frond. It is a large plant, and though not as large as the last, grows up to 10 ft. long. It occurs between low-tide mark and 12 fathoms (Fig. 116).

FIG. 113.—*Laminaria saccharina.* Two mature plants. The footrule shows the comparative size.

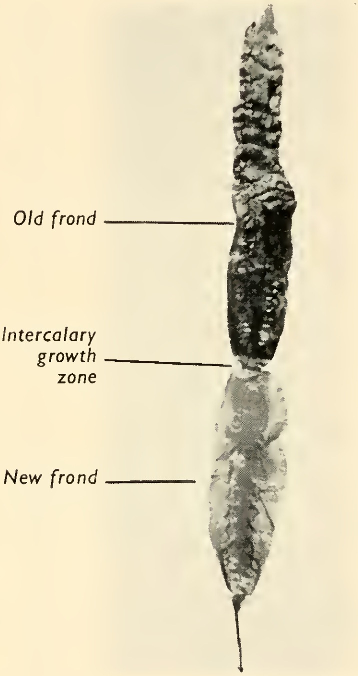

FIG. 114.—*Laminaria saccharina.* Mode of growth of the frond.

In all species the expanded lamina has no midrib and is borne on a basal stipe, which is attached to the rock surface by a holdfast of very variable form. This holdfast is made up of a number of separate branches of decreasing thickness which adhere very tightly, forming flattened discoid masses immediately in contact with the rock and attached by densely packed rhizoids. The lamina grows from a meristematic zone at its base, which annually forms a new frond, displacing that of the previous season, which then dies off.

Many of the species are used as food in Asia, especially by the Chinese, Japanese and Russians. In Japan about ten species are eaten, and the gathering between July and October is an important industry. These kelps contain considerable quantities of Iodine, which is important for the functioning of the thyroid gland, and it is a noticeable fact that goitre is almost unknown among the Japanese. Apart from their use as food the kelps are perhaps the most important commercial source of Iodine, which is extracted from the ash after the weeds have been burned.

Fig. 115.—*Laminaria digitata.* Entire plant.

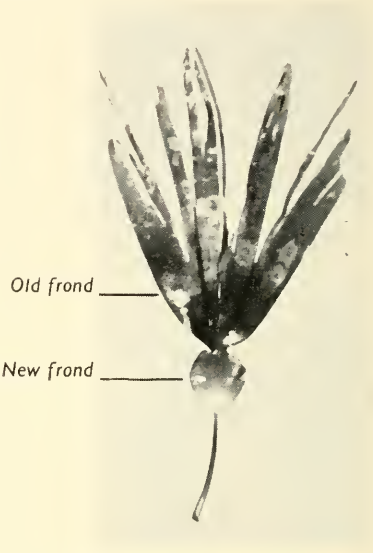

Fig. 116.—*Laminaria hyperborea.* Plant showing development of new frond at base of old frond.

Structure of the Thallus

The thallus of *Laminaria* shows an exceptionally complex structure, the most elaborate in any group of the Algae. Anatomically stipe and lamina are alike and both show a separation into three distinct zones (Fig. 117) although these are more clearly marked in the stipe owing to its greater thickness. The stipe may also show annual zones of growth. Near the apex the blade is only one cell thick, but it soon becomes two-layered, after which the primary tubes are formed, which constitute the **medulla** and separate the two **external layers**. By division of the cells of the outer layers parallel to the surface a zone of **cortex** is cut off. These cortical cells then elongate longitudinally and the common walls between them swell and so separate the cells from one another, except at certain points of union where they become drawn out into short secondary tubes. In this way three separate zones of tissue become differentiated. On the outside lies the external layer, the cells of which are primarily concerned with assimilation. These divide only perpendicular to the surface. Inside this comes the cortex, composed of elongated cells separated from one another by mucilage, and finally in the middle is the central medulla composed of larger, longitudinally running filaments whose function appears to be primarily that of conducting materials in solution. In the stipe these zones can be clearly seen.

The cells of the medulla may become greatly modified. This applies particularly to certain cells which cease to divide at an early stage (Fig. 118). They are drawn out by the growth of the tissues, into long straight filaments, considerably attenuated, except at their ends, which retain the original width, thus producing the appearance which has given them the name **trumpet hyphae**. The end walls are penetrated by numerous protoplasmic connections, sometimes sheathed in callus, which later extends to cover both sides of the perforated plate. The structures have been compared to the sieve tubes of higher plants (see p. 467) (Figs. 119 and 120).

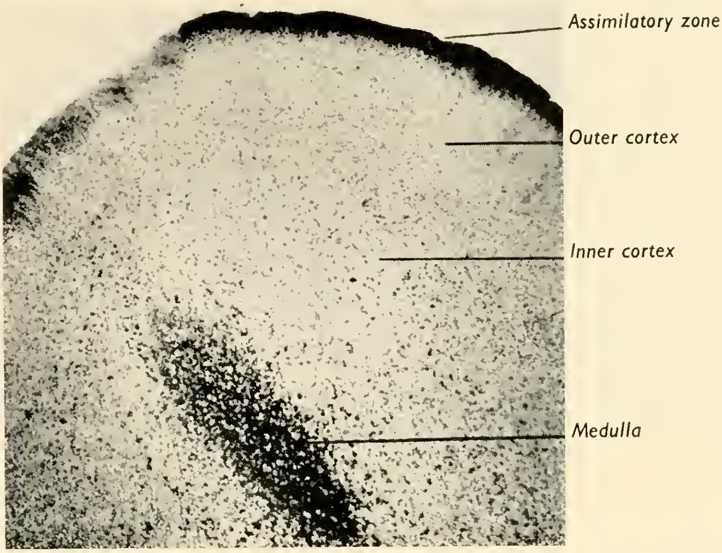

FIG. 117.—*Laminaria digitata*. Transverse section of stipe.

Apart from this the trumpet hyphae possess spiral bands of cellulose thickening on their walls, a feature which again recalls the thickening of a wood vessel (see p. 465). The function of these trumpet hyphae is still uncertain. Many suggest that they serve for conduction of fluids, while others think of them as storage organs, and others again prefer to regard them mainly as organs of support. It may be pointed out that pitting is not restricted to the trumpet hyphae, as in some species other cells in the inner cortex occur with pitted walls, similar to those in the medulla. These may also facilitate the diffusion of food material.

A system of anastomosing, intercellular mucilage ducts occurs in the stipe and frond of several species, but only in the fronds of *L. saccharina* and

L. digitata. There are periodic openings from these ducts to the exterior and they are lined with isolated groups of secretory cells. They arise schizogenously between cells of the surface layer and deepen and extend with growth, becoming connected with each other into a continuous network.

Fig. 118.—*Laminaria digitata.* Trumpet hypha in medulla showing the enlarged ends of two hyphae in contact and the transverse ribbing of the hyphae.

The structure of the attaching organ or holdfast is markedly different from the rest of the thallus. Growth is localized in the apices of the branches which spread out in contact with the rock. It differs anatomically by the absence of a medulla and of trumpet hyphae.

Asexual Reproduction

The asexual reproductive organs are developed in widely extended **sori,** which may cover the greater part of the surface on both sides of the lamina (Fig. 121). The **zoosporangia** arise from the superficial cells in the following way. Each cell divides into two, forming a basal cell and a terminal cell. The terminal cell is at first assimilatory, but later enlarges considerably, becomes club shaped and is invested at the top by a mucilaginous cap. This body becomes a **paraphysis,** and the caps of all the paraphyses adhere and serve to keep them together. Meanwhile the basal cell enlarges laterally and from its outer ends cuts off two cells, one on each side of the terminal cell. Each enlarges considerably, becomes oval and forms a sporangium. These sporangia thus come to lie between the paraphyses, and the whole is covered by the mucilage derived from the latter. Inside the zoosporangium thirty-two **zoospores** are differentiated, and are finally liberated through the apex of the sporangium. According to most workers these zoospores are all of the same size, though in one or two cases zoospores of different sizes have been described.

The zoospores are almost pear-shaped bodies with two long, laterally placed flagella, and each may possess a tiny eye spot. They are actively motile but soon settle down and germinate.

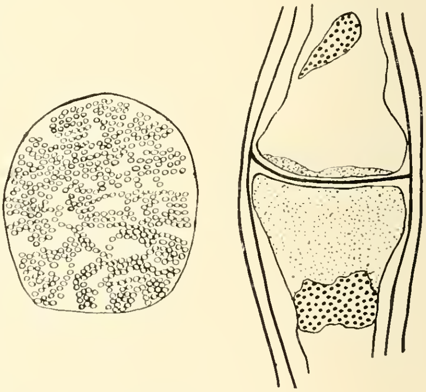

Fig. 119.—*Laminaria saccharina.* On left the surface view of the sieve plate in a trumpet hypha. On right an old trumpet hypha with callus accumulated on the sieve plate. (*After Sykes.*)

THE GAMETOPHYTES

The result of germination is the formation of very small male and female gametophytic plants, both of which are filamentous and differ completely from the sporophytic thallus. They also differ from each other in shape and size.

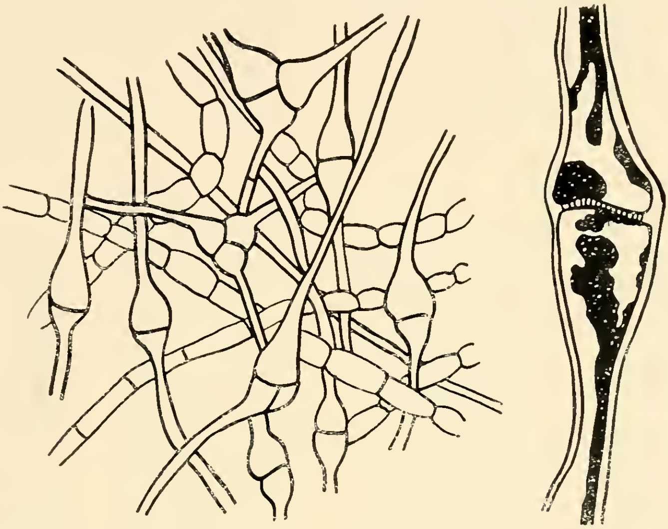

FIG. 120.—*Laminaria sp.* Longitudinal section through part of the medulla of the stipe showing trumpet hyphae and septate transverse filaments. On the right a single trumpet hypha showing sieve-like perforation of the seed plate.

On germination the zoospore first forms a tube which terminates in an

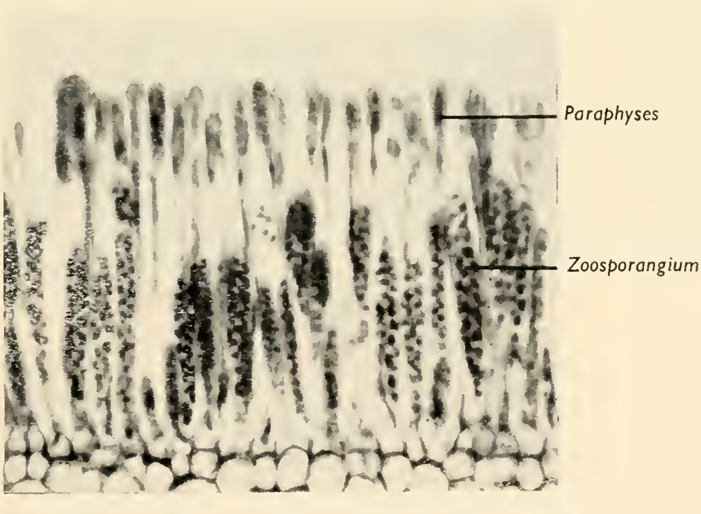

FIG. 121.—*Laminaria digitata.* Zoosporangia on surface of the thallus.

enlargement into which the contents of the zoospore migrate. The nucleus in the zoospore divides, and one daughter nucleus passes into the enlargement while the other degenerates. The cell formed by the enlargement divides several times, and the mature gametophyte consists of a short filament of cells with shorter branches. It may even be reduced to two or three cells. The **male gametophyte** is composed of smaller cells than the **female gametophyte** (Fig. 122).

The sex organs arise from the lateral branches. The **antheridium** is a small, more or less spherical, cell which gives rise to one **antherozoid**. This antherozoid is a small, oval cell provided with a pair of fairly long, unequal, laterally placed flagella. The **oogonium** is also formed from a cell of a lateral branch, inside which is a single **oosphere**. The oogonium is surrounded by a thick mucilaginous investment which is prolonged at the apex into a cup comparable with an egg cup. The oosphere emerges from the oogonium and lies in the cup with the greater part of the oosphere exposed.

Fertilization is effected in the usual way by the migration of the antherozoid to the oosphere and the union of the male and female nuclei, after which a wall is formed around the oosphere, resulting in the formation of an **oospore.** Male and female gametophytes are found in equal numbers, and it has been shown experimentally that from any zoosporangium an average of sixteen male and sixteen female gametophytes will be produced. It follows that normally each oosphere should become fertilized, and this takes place quite rapidly. Should the oosphere fail to receive a male gamete it may be capable of independent development producing a parthenogenetic sporophyte.

The development of the oospore begins with its division into two cells, from which is produced a filament with an apical cell. At first the young plant remains attached to the top of the oogonium, but it later becomes detached and one or more of the basal cells of the filament elongate into unicellular rhizoids which form the primary attachment to the substratum. Next the upper part widens into a monostromatic blade on a filamentous stipe. The blade then becomes distromatic and the stipe becomes polysiphonous. A new meristematic region appears between stipe and blade ; apical growth gradually ceases and the apex of the frond is eroded. The first appearance of the cortex is as a single layer of cells between the two layers of the blade. The cells are large and parenchymatous, and are increased by the addition of new cells in the meristematic zone. The medullary hyphae appear as the cortex becomes double-layered, and the expansion of the trumpet hyphae takes place in the intercellular spaces.

Alternation of Generations

Laminaria thus exhibits an alternation of generations comparable with that in *Dictyota*, but whereas in *Dictyota* the two generations are morphologically alike, in *Laminaria* the gametophyte is reduced to a minimum, producing little more than the essential sex organs, while, on the other hand, the sporophytic generation shows the greatest tissue elaboration found in the

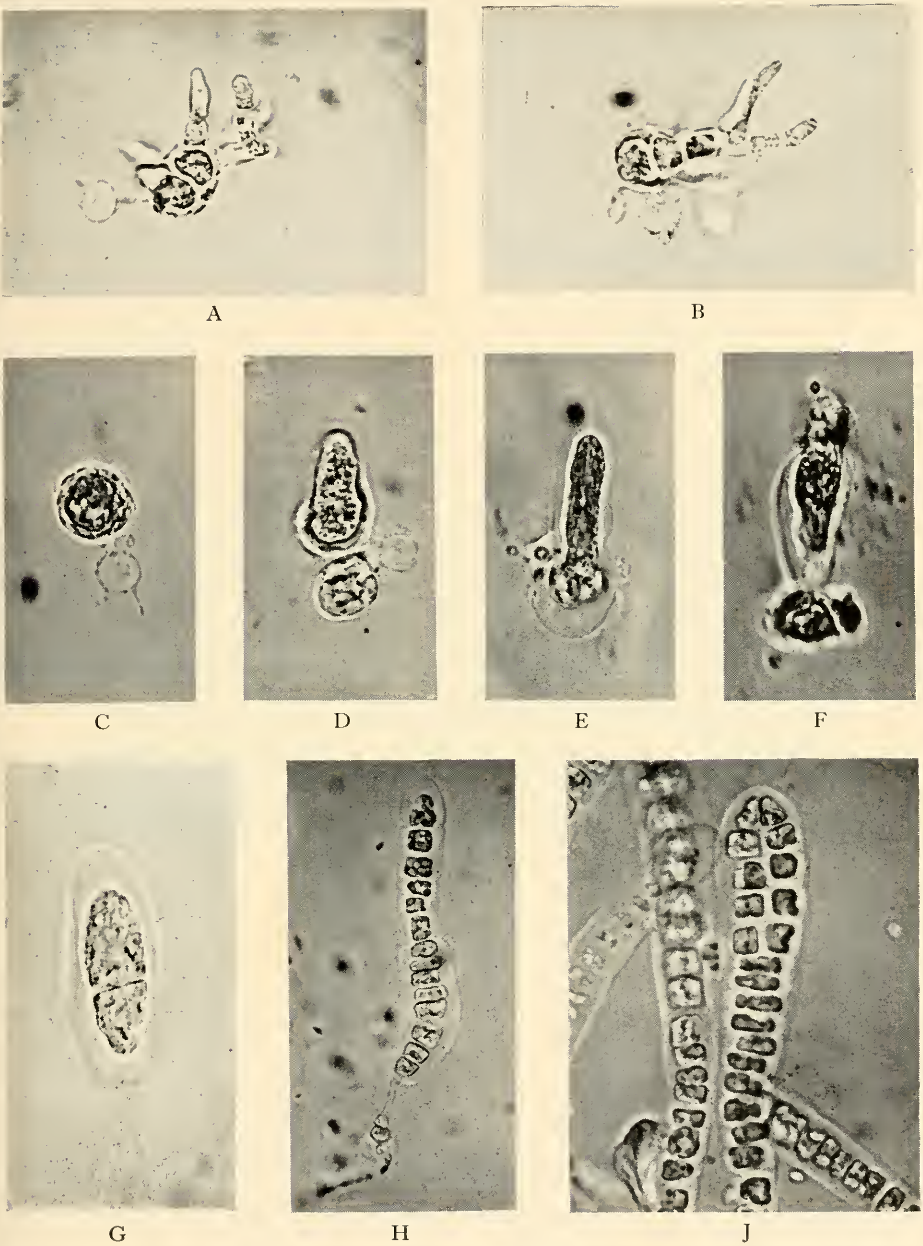

FIG. 122.—*Laminaria saccharina.* Gametophytic generation. A, Two-celled male thallus showing on the left the empty wall of the zoospore and on the right antheridial branches. B, Three-celled thallus with antheridial branches on right. C, First cell of female thallus attached to empty wall of zoospore. D, One-celled female thallus with oogonium. Oosphere emerging at top. E, Elongated oosphere. F, Antherozoids attached to the protoplasm of the oosphere. G, Two-celled zygote. H, Primary filament of young sporophyte. J, Older stage of young sporophyte showing apical growth.

(*From slides lent by Professor L. Newton.*)

Phaeophyceae. It must not be thought, however, that there is a definite progression within the Phaeophyceae towards a reduction of the gametophyte, for in certain other orders the gametophyte is large and fairly elaborately developed, while the sporophyte is reduced to a filamentous structure bearing the zoosporangia. It might appear therefore that in the Phaeophyceae there have been two contrasting tendencies operating, the one to reduce the sporophyte and the other to reduce the gametophyte.

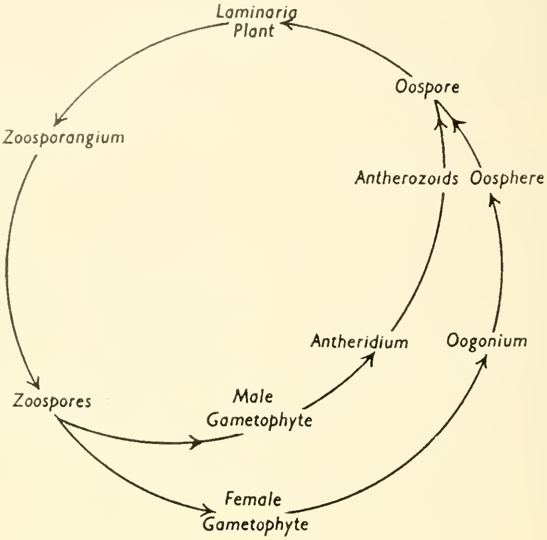

Fig. 123.—Life-cycle of *Laminaria.*

We may represent the life-cycle of *Laminaria* in the above diagram, which, it will be seen, does not differ in any essential from that of *Dictyota* except in the size of the various structures (Fig. 123).

Fucales

The Fucales are Phaeophyceae in which the reproductive organs are borne in special cavities in the surface of the thallus, termed **conceptacles.** Growth is by means of an apical cell ; the thallus is large and composed of an elaborate system of filaments held together by mucilage. There is no morphological alternation of generations, although a cytological one has been shown to be present. The plant itself is diploid. The reduction division occurs prior to the formation of the gametes, which are therefore monoploid, while the fertilized zygote is again diploid. There is no asexual method of reproduction. Sexual reproduction is oogamous.

We shall consider the life-history of *Fucus* as an example of this order.

Fucus

Fucus is a very common Brown Alga which occurs all round the British coast attached to rocks (Fig. 124), and lives between high and low tide marks, the various species showing distinct zonation. It is attached to the rocks by means of a specialized basal disc called the **holdfast.** The thallus is dark brown in colour or almost black when dried, and is dichotomously branched, the lower part being narrow and almost round, while the upper parts are flatter and broader but with a thick midrib (Figs. 125 and 126). The plants vary considerably in size according to the conditions under which they are growing. If the plants are living on exposed and rather dry situations near high-tide mark they are rarely more than 6 in. in length, but if living under conditions of more complete immersion they may be anything up to 3 ft. in length, according to their age.

FIG. 124.—Photograph showing the growth of *Fucus* on rocks of the foreshore, Ventnor, I.O.W.

When the plants are in a reproductive condition the ends of the branches become enlarged and covered with tiny wart-like projections, each of which has a minute pore at the centre. These bodies mark the position of cavities in the tissue of the thallus, which are called **conceptacles,** and in which the reproductive organs are borne (Fig. 127). At the tip of each branch there is a small groove, at the bottom of which lies the single four-sided apical cell by means of which the thallus grows. The apical cell cuts off broad segments on two sides and thinner segments on the sides at right angles to the first, thus producing a flattened thallus. From time to time it also divides equally into two halves, thus starting a dichotomy of the shoot. Cells are also cut off from the base of the apical cell and these become the medullary filaments. In *Fucus* we have an example of an Alga which grows only at the tips of the fronds. The cells cut off from the apical cell form at first a close tissue, but lower down the central ones elongate into filaments, while the superficial layers remain parenchymatous.

FIG. 125.—*Fucus vesiculosus.* Plant showing air bladders. Much reduced.

FIG. 126.—*Fucus serratus.* Plant showing toothed margins, and fertile regions at end of branches. Much reduced.

Because it possesses an apical cell the thallus structure of *Fucus* is usually placed in contrast with the filamentous and trichothallic growth of lower types like *Ectocarpus* and *Cutleria*, but in reality it is based upon a filamentous plan.

The young plant has a group of apical hairs, formed at the growing point, each of which has a basal region of active cell division. At a later stage one or more of these hairs, usually that in the centre, dies off to its base, and the basal cell gives rise to the apical cell of the future thallus.

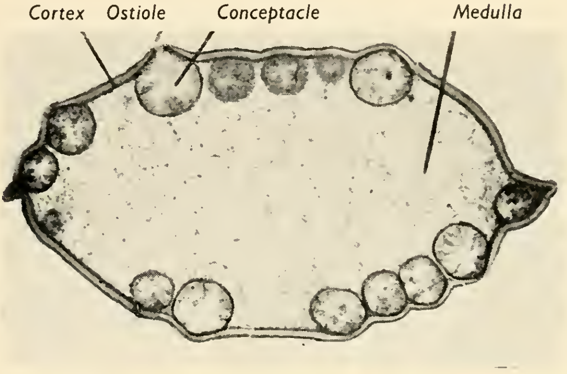

FIG. 127.—*Fucus vesiculosus.* Transverse section through fertile tip of frond showing cortex, medulla and numerous conceptacles.

When the thallus is injured the inner tissue near the wound grows out into a tuft of hairs and the same process is repeated, producing an apical cell from which new tissues are regenerated.

Scattered along the length of the thallus in close association with the thickened midrib are **air bladders,*** which serve very much the same function as the air spaces which we shall meet with in certain aquatic flowering plants, namely, that of assisting the plant to float.

Small tufts of hairs grow from cells in the apical groove and also from small cavities, called **cryptostomata,** scattered over the surface of the thallus. These hairs may act as absorbing organs.

STRUCTURE OF THE THALLUS

The anatomy of the frond of *Fucus* shows little difference in structure wherever we may cut it, that is to say, that except for a variation in the quantity of the tissues the structure is the same throughout the length of the thallus. The external layer consists of small rectangular cells with abundant plastids, which give them a dull brownish colour, and it is in this layer that the bulk of the assimilation takes place. The cells of this layer remain capable of active division all over the plant. Within this external layer comes a varying thickness of **cortex** composed of thin-walled parenchymatous cells. These also continue to divide actively, so that the cortex increases in thickness towards the base of the plant. The inner cortical cells also grow out into thick-walled **hyphae,** which grow in among the original filaments of the central zone or **medulla,** filling this space with a mass of closely interwoven

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* These are absent in some species.

cells, among which the original filaments can be picked out by their thin walls. Towards the base, in the region of the stipe, the medulla contains nothing but these thick hyphae, and the same is true of the flattened edges of the thallus.

The original medullary filaments are to be seen in the midrib of the thallus, and they run more or less straight vertically, recalling the similar elements in *Laminaria*. They are said to act as food-conducting elements and their cross walls are probably perforated, like sieve-plates in the higher plants. Thus we see that *Fucus* contains tissues which are specialized for absorption, photosynthesis, conduction and attachment respectively, which implies a remarkably high grade of organization for one of the Thallophyta.

We must clearly distinguish between the growth in length of the thallus, which takes place only through the apical cell, and increase in the thickness of the branches, which is brought about by growth and division of existing cells. The cells which make up the medulla are, moreover, not closely packed together, as is true of the tissues of higher plants, but embedded together in mucilage, with the result that these seaweeds are generally extremely slimy to handle and are capable of shrinking or swelling to a surprising extent with variations of the water content. Some species can lose more than 50 per cent. of their weight by drying without being injured.

In *Fucus* there is no asexual method, but reproduction through vegetative propagation may take place by the regeneration of the missing parts from bits of the thallus which are broken off from the parent plant.

Sexual Reproduction

The reproductive organs develop within the conceptacles. In some species only one kind of reproductive organ develops in any one conceptacle, and in such instances, moreover, the sexes are separated on different plants. This varies in different species; in some, *e.g.*, *F. serratus*, the two kinds of sex organs are found on different plants; in others, *e.g.*, *F. spiralis*, both types of sex organs may occur in the same conceptacle. The gametes are of two quite distinct types, that is to say, the plants show an advanced condition of oogamy (Figs. 128 and 129).

The **conceptacles** arise from superficial cells very near the growing point. A cell becomes depressed below the surface and then divides transversely. The upper cell elongates like a tongue towards the opening of the depression and degenerates early, while the lower cell divides vertically to form a group of cells which become the lining layer of the mature conceptacle. In some other members of the Fucales, *e.g.*, *Himanthalia*, the upper cell forms a typical multicellular hair, while in *Pelvetia* it forms a group of hairs. The suggestion of a connection with the cryptostomata or sterile hair-pits is obvious.

The sex organs consist of **oogonia** and **antheridia.** The oogonium arises from a superficial cell of the conceptacle, which divides to give a basal cell and an oogonial cell (Fig. 130). The basal cell divides no more, but the oogonium enlarges and its nucleus divides into eight, with reduction of the

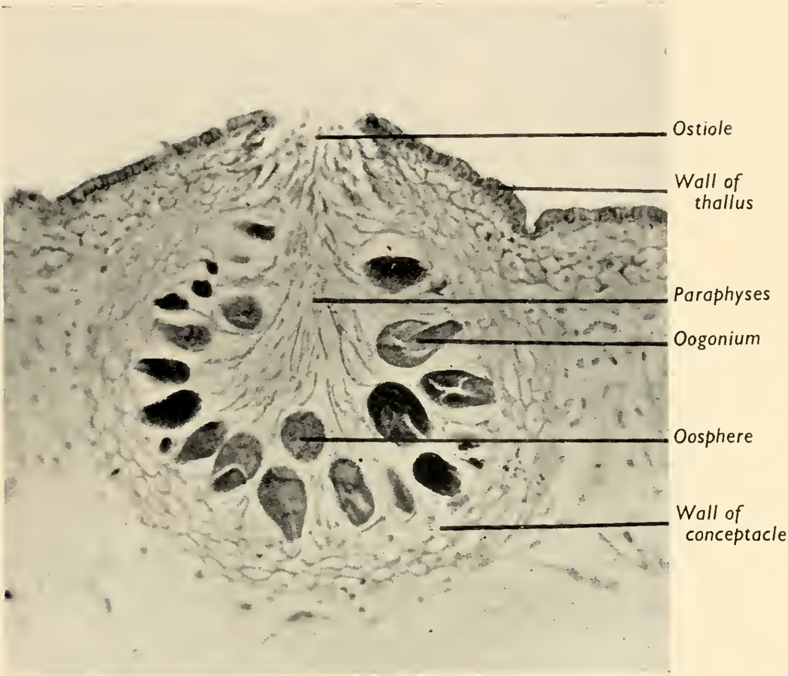

FIG. 128.—*Fucus serratus.* Transverse section of a female conceptacle showing development of oogonia.

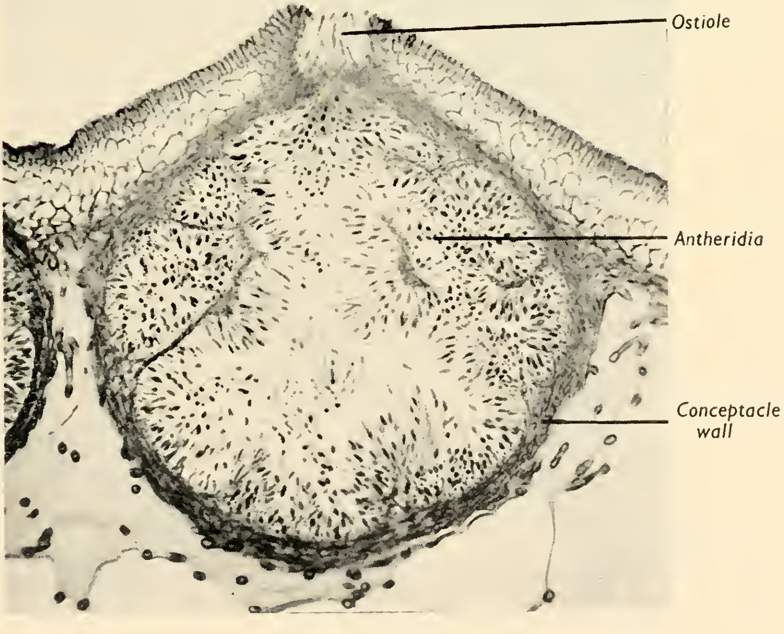

FIG. 129.—*Fucus serratus.* Transverse section of a male conceptacle showing antheridia on branched filaments.

chromosome number to one half. The eight nuclei separate and the cytoplasm splits into eight portions, each with one nucleus. Each of these eight cells is termed an **oosphere.** When they are mature the outer wall (**exochiton**) of the oogonium breaks and the eight cells are liberated as a package contained in an inner wall (**mesochiton**). In the sea water this inner wall also opens, and the innermost coat of mucilage (**endochiton**) disperses and the eight oospheres escape as passive spherical bodies. Each oosphere contains many plastids, giving it an olive-green colour. Interspersed with the oogonia in the conceptacles are long sterile hairs, or **paraphyses,** which arise all over the surface of the walls of the conceptacle, while their free ends project out of, or at any rate towards, the pore or **ostiole** of the conceptacle.

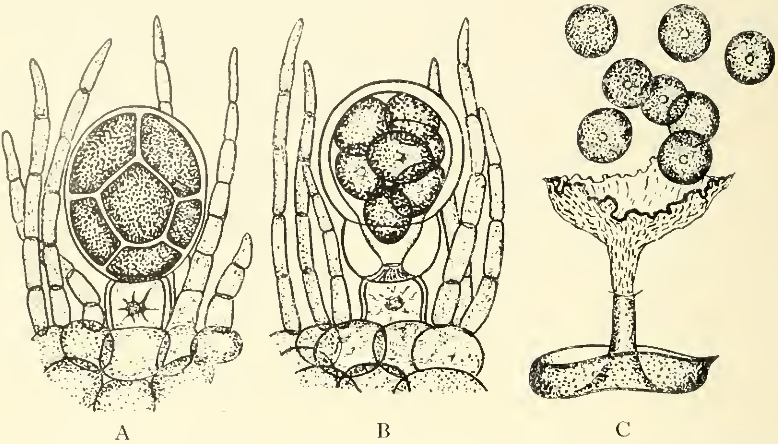

Fig. 130.—*Fucus serratus.* A, Mature oogonium containing eight oospheres. B, Liberation of packet of oospheres from outer wall of oogonium. C, Liberation of separate oospheres by solution of endochiton. (*After Thuret.*)

The male reproductive organs or **antheridia** arise in much the same way as the oogonia from the surface of the male conceptacles. A superficial cell grows into a short branched structure, with both sterile and fertile branches (Fig. 131). The latter are the antheridia. The conceptacle is almost filled by

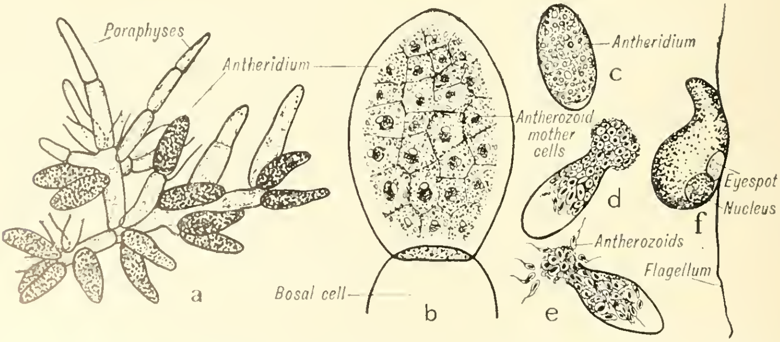

Fig. 131.—*Fucus serratus.* A, Antheridia on a branched filament. B, Ripe antheridium. C, Detached antheridium D and E, Liberation of antherozoids. F, Antherozoid. (*After Thuret.*)

these densely branched structures. At first the antheridium contains a single nucleus, but this is rapidly increased by division until sixty-four are formed. Around each nucleus a membrane is formed, enclosing a small quantity of protoplasm and a single orange chromoplast ; thus sixty-four **antherozoids** are formed. Each is pear-shaped and has two lateral flagella, one forward and one backward. They are unequal, with the shorter flagellum forwards, contrary to the general rule among the lower Phaeophyceae. The orange-coloured chromoplasts give a bright colour to the mass of antherozoids which escape through the ostiole.

The antheridium, like the oogonium, has a multiple wall, though its layers are not so clearly defined. The outer wall opens apically and releases an oval inner sac, containing the antherozoids, in which they emerge through the ostiole of the conceptacle. This inner sac then swells and opens at its ends, and the antherozoids swim out into the sea water.

The oospheres and antherozoids are liberated with a quantity of mucilage at ebb-tide and are picked up by the advancing edge of the flood-tide, and it is here that fertilization takes place. The membrane around the antherozoids bursts when they have been liberated from the conceptacle, and they swim off by means of their flagella. The antherozoids soon seek out an oosphere, and immediately attach themselves to its surface in large numbers. They attach themselves by the tips of the anterior flagella and the movements of the posterior flagella cause the oosphere to rotate in the water, with its attached swarm of males. Eventually one antherozoid penetrates the oosphere and its nucleus travels inwards through the cytoplasm and fuses with that of the oosphere. The resulting zygote immediately secretes a wall which prevents penetration by any other antherozoid and becomes an **oospore.** The wall of the oospore is mucilaginous and fixes it to the substratum before growth begins. After twenty-four hours it begins to divide, the nucleus dividing first, followed by the laying down of the first cell wall between the daughter nuclei. This wall is invariably at right angles to the

FIG. 132.—*Fucus serratus.* A series of stages in the early development of the frond from a fertilized zygote.

direction of the incident light. The lower of the two cells contains few plastids and develops into the holdfast while the rest of the plant grows from the upper cell. As growth continues a few filaments of cells develop at the lower end and form what are called **rhizoids,** while at the other end the thallus, which is at first rounded, becomes flattened. The plant soon becomes permanently anchored to a rock or similar support by the aid of the rhizoids, from which later the holdfast is developed (Fig. 132).

In the life-history of *Fucus*, therefore, we see a highly developed sexual method of reproduction, which is not associated with any kind of asexual one. The life-cycle may therefore be represented by the diagram (Fig. 133).

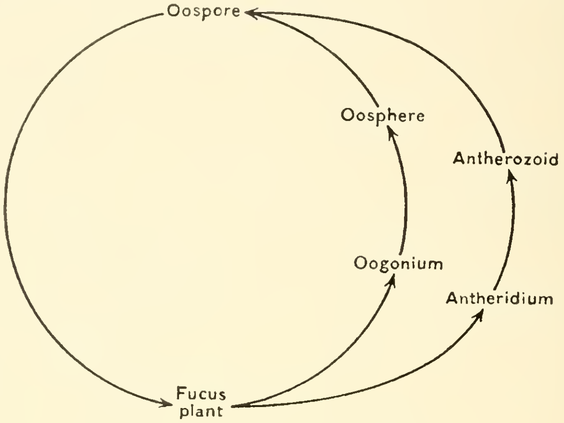

Fig. 133.—Life-cycle of *Fucus*.

It is interesting to note that in certain closely allied genera not all the eight oospheres mature, although in every case eight nuclei are produced in the oogonium. In the genus *Ascophyllum* four out of the eight nuclei function, forming the nuclei of four oospheres, while in *Pelvetia* two oospheres are formed, and in *Sargassum*, the floating Sargasso Weed, only one out of the eight develops into an oosphere. The fact that in every case eight nuclei were produced led to an investigation of their cytology, and it was found that the reduction division occurred in the first divisions of the oogonium and antheridium, so that the mature oosphere and antherozoid in each case is a monoploid structure. Reduction division immediately preceding the formation of the gametes is common in animals, but in plants it usually occurs either in the formation of the asexual spores or after germination of the zygote, and in this respect *Fucus* is exceptional—a point possibly associated with the absence of any method of asexual reproduction.

It may occasion surprise that a diploid plant like *Fucus* should bear gametes, which appears to contradict what has previously been said about the laws of alternation of generations (p. 110). The paradox is explained by the suggestion that the initial cell in both oogonium and antheridium is really a sporangium, which proceeds directly to the formation of gametes without any intervening vegetative stage (cf. *Ectocarpus*, see p. 115). This is not so far-fetched as might be supposed, since the same thing is well known to occur in the Angiosperms, where the whole gametophyte generation has certainly been reduced to the gametes only, which therefore appear to be borne upon the sporophyte plant. *Fucus* is a parallel case, the gametes being formed precociously from the contents of the sporangia themselves. In other genera of the Phaeophyceae, notably in *Laminaria*, stages on the way towards this reduced condition of the gametophyte may be found, the sexual generation consisting of a mere half-dozen cells on which the gametangia are borne, and cases of the precocious germination of zoospores still in the zoosporangium are known. The interpretation of the antheridia and oogonia as double structures is also corroborated by the multiple nature of their walls.

Traces of the formation of septa in the development of the oospheres and antherozoids have been cited as telling against the above view, because the sporangia of the Phaeophyceae are never septate. If, however, the sexual structures really represent sporangia enclosing a single gametangium, which constitutes the whole gametophyte, then we would expect to find vestiges of septation in their contents, since the gametangia of the lower Phaeophyceae, *e.g.*, *Ectocarpus*, are definitely multicellular.

BACILLARIOPHYCEAE

This group of Algae is markedly distinct from any other and has long been a favourite with naturalists on account of the beauty and symmetry of the sculpturing on the cell walls. Under the old name of " Diatoms " they figure prominently in every book on microscopy, and it is not too much to say that their study contributed greatly to the development of the modern microscope.

They are entirely unicellular, though the cells sometimes hang together in chains or groups, and the cell wall is of transparent silica, formed in two halves which fit together like a box and lid. On solid surfaces the protoplasm can quit its shell and live naked for a time. The cell contains plastids of a bright yellowish-brown colour, due to a yellow pigment called **diatomin,** which may, however, be only a form of the fucoxanthin of the Brown Seaweeds. It is therefore the peculiar structure of the cell wall, rather than the pigmentation, which separates this group from the Phaeophyceae. Apart from diatomin, chlorophyll, carotin and xanthophyll are also present, as in other groups. A fatty oil is formed as the sole product of photosynthesis and the drops are usually conspicuous in the cell, accompanied by grains of volutin.

The Diatoms are an immense and varied group. They abound in all natural waters, both fresh and salt, and seem to flourish ubiquitously wherever nature presents a damp surface. They can often be seen as a yellow scum on the surface of mud in ditches, while, on the other hand, they are the most important group of plant organisms in the **plankton** of the sea, that is the population of passively floating microscopic life which fills the surface layers of all the oceans and forms the " pasture " of the fishes. As the siliceous cell walls are almost indestructible there are many beds of fossil diatoms known, formed in ancient seas, which produce the fine powders used commercially for polishing, called Diatomite or Kieselguhr.

There are two Orders in this group :—

1. **Centrales,** in which the shape of the cell is similar to that of a circular pill-box. These are predominantly marine.
2. **Pennales,** in which the cell is elongate and boat-shaped (naviculoid) in outline. They occur predominantly in fresh waters.

As a type we shall select one of the latter, an uncommonly large form which is very widely distributed in ponds and ditches.

Pinnularia viridis

Several closely related species such as *Pinnularia nobilis and P. major* are also covered by the following description.

The cells are elongate-elliptical in outline, seven to eight times as long as broad and with rounded ends (Fig. 134). The usual size is about $20 \times 140\mu$. The siliceous wall or **frustule** is in two halves, the **valves,** corresponding to a box and lid. The species is unique among Diatoms, in being enveloped in a wide mucilaginous capsule. The view looking down on the lid is called the **valve view,** and that from the side, where the margins of the box and lid meet, is called the **girdle view.** From the side the cell looks rectangular. Each valve itself consists of two closely united but separable portions, *i.e.*, the flat **valve face** and the **mantle,** which forms part of the girdle side of the cell. The mantles of the two valves do not overlap each other but are connected by a separate **girdle band** (Fig. 137).

Each valve face has a clear median strip running from end to end, in which are three thickened spots, the **central nodule,** and two **polar nodules,** connected by a very narrow slit, the **raphe.** On each side of the median strip is a row of parallel transverse ribs, or **costae,** very prominently marked. The girdle side of the frustule is unmarked except for the ends of the costae which appear at its edges (Fig. 135).

The costae are really hollow channels in the thickness of the frustule with an opening inwards and containing pectin and cytoplasm. The raphe is a very narrow slit, bent as shown in the section illustrated in Fig. 137, and penetrating the cell wall, though there may not be a clear channel right through. At the nodules it follows a twisted and very complex course. Inside the siliceous coat, in the living cell, is an inner wall of pectin, within which is a utricle of cytoplasm, surrounding a large central vacuole, and two very large plastids, each as long as the cell and occupying the whole breadth of the girdle on each side of the cell. In each plastid there is one **pyrenoid.** The nucleus is centrally placed (Fig. 136).

REPRODUCTION

When a diatom cell divides, nuclear division is followed by the separation of the two valves and the cleavage of the cytoplasm into two parts. Each

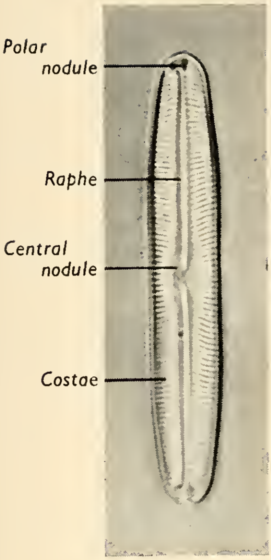

Fig. 134.

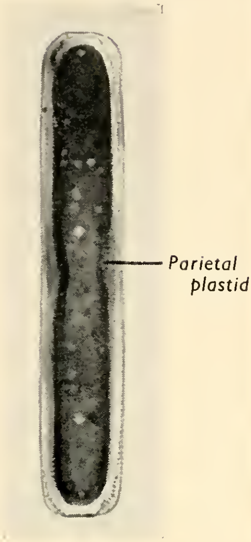

Fig. 135.

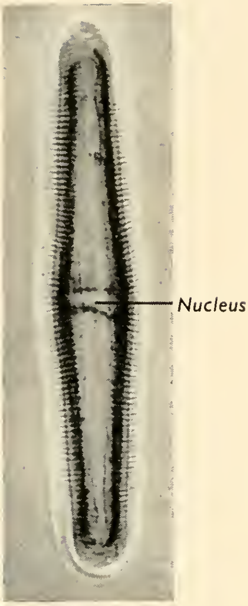

Fig. 136.

Fig. 134.—*Pinnularia viridis.* Valve view of frustule.
Fig. 135.—*Pinnularia viridis.* Girdle view showing broad parietal plastid.
Fig. 136.—*Pinnularia viridis.* Valve view in optical section showing the centrally placed nucleus and the edges of the two lateral plastids.

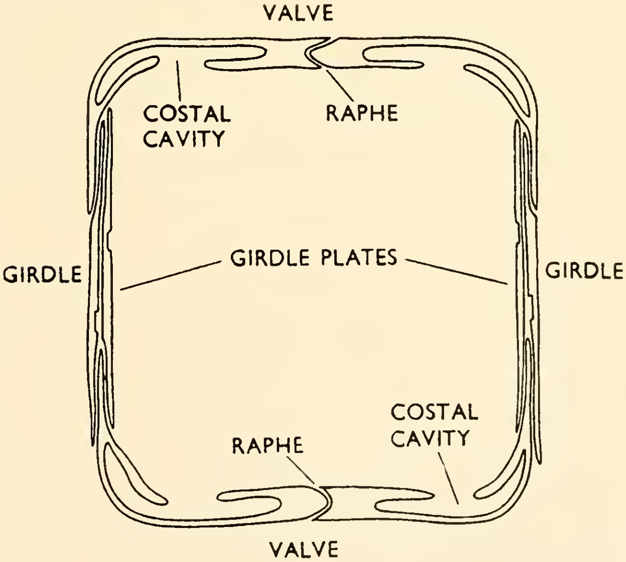

Fig. 137.—*Pinnularia viridis.* Transverse section of the frustule showing structure of the valves and girdle plates. (*After Muller.*)

half has therefore one valve of the old cell and one naked side, which it covers by secreting a new valve fitting *inside* the old one. One daughter cell therefore remains the same size as the parent, but the other, which took the smaller valve with it, is slightly smaller. Thus in successive cell divisions one line of daughter cells becomes progressively smaller. As this cannot go on indefinitely a restorative process eventually occurs. The cell secretes abundant mucilage, which forces the valves apart, and the liberated protoplast grows to the maximum size of the species and then forms two new valves which reconstitute a new cell. This liberated protoplast is called an **auxospore.**

In many other Diatoms auxospore formation is associated with conjugation, but sexual reproduction is not known to occur in *Pinnularia*. In related forms, *e.g.*, *Cymbella*, two individuals cohere and become enveloped in mucilage (Fig. 138). In each cell the nucleus divides into four, presumably with chromosome reduction, and two of the nuclei in each cell abort. Each protoplast then divides into two and fusion takes place, by two and two, between the conjugating protoplasts. The two fusion cells formed then function as auxospores and secrete new frustules.

Reference has been made above to the probable occurrence of meiosis preceding conjugation. Although this has not been definitely proved in all cases it is generally believed that the cells are diploid, as no reduction is known to occur after conjugation. Somatic divisions are mitotic and follow normal lines, except for the presence of a **centrosome** from which the spindle originates.

Pinnularia shows a power of creeping movement on a solid substratum which is well seen in specimens mounted on a glass slide. This seems to be due to protoplasm extruded through the raphe and circulating along the surface of the valve, returning through openings in the polar nodules, thus providing a sort of gastropodous movement, rather like that of a tank-track. The motion of the protoplasm can be demonstrated by mounting the cells in a suspension of Indian ink or Carmine. The external protoplasm may be in two layers, as opposing currents of granules can be seen on the same surface.

Plankton

Mention has been made of the importance of the Diatoms as constituents of the marine plankton. They are also abundant in fresh-water plankton, though this is of minor importance compared with that in the sea. In coastal waters their development follows a well-marked annual cycle. In April occurs a great vernal outburst of Diatom life, which rapidly depletes the reserves of phosphate, nitrate and dissolved silica in the sea water and leads to a midsummer dearth. Meanwhile the dead cells have sunk and decayed in deeper waters, releasing their stores of absorbed nutriment. Some of this is restored to the surface by the disturbance of autumnal gales, producing a minor secondary maximum in September and October. This is followed by another minimum during the winter. Meanwhile the chilled surface water, being denser, sinks and displaces the warmer deep water with its stores of accumulated food materials. The surface waters thus become again rich in the materials of life, and the vernal outburst once more appears with the increasing solar radiation in spring.

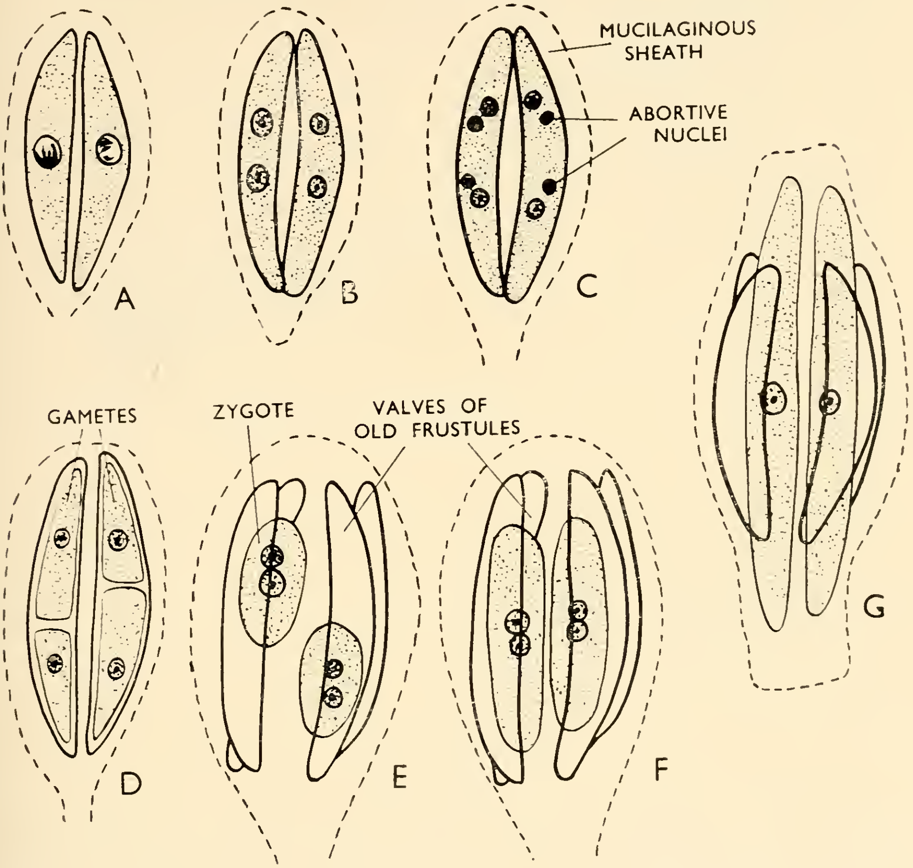

Fig. 138.—*Cymbella lanceolata.* Sexual conjugation. A, Two naked protoplasts enclosed in a mucilaginous envelope. B and C, Nuclear divisions. D, Division of the protoplasts. E, Fusion of the protoplasts to form two zygotes. F and G, Enlargement of the zygotes to form the protoplasts of two new cells. (*After Geitler.*)

Many oceanic Diatoms show peculiarities, such as fringes of long spines, or marginal membranes, which are interpreted as flotation devices. One of the commonest of these is the attachment of cells together into chains by means of interlocking processes on the frustules. The dominant species of plankton Diatoms vary in different areas of the sea. Round the British Isles species of a circular type, *Coscinodiscus*, are predominant. Diatom frustules form the chief oceanic sediment in Antarctic latitudes, where the " Diatomaceous ooze " covers many thousands of square miles of the ocean bed.

RHODOPHYCEAE

The Rhodophyceae are Algae in which two pigments, **phycoerythrin** and **phycocyanin** are present in addition to chlorophyll. Variations in the relative amounts of these pigments produce corresponding variations in colour between pure red and dark purple, although the group is commonly called the Red Algae.

The Rhodophyceae are, on the whole, more complex than the Phaeophyceae. No unicellular types occur, and the thallus consists of a system of filaments, sometimes simple, but more often forming a complex, corticated body, built either on a single central filament or on a medulla of interwoven filaments like that of *Fucus*. The reproductive organs are often very elaborate. The male gametes are non-motile and depend on the water carrying them against special receptive outgrowths of the female organs, which are generally enclosed in the thallus tissues. After fertilization various complex growth processes may take place before spores are produced. These spores on germination may give rise to fresh sexual plants, but more often they produce asexual individuals on which tetraspores arise. In the latter forms an alternation of generations exists, somewhat similar to that found in the Phaeophyceae.

The Rhodophyceae are divided into a number of orders of which we shall consider examples of the following :—

1. **Nemalionales** (*e.g.*, *Batrachospermum*).
2. **Gigartinales** (*e.g.*, *Chondrus*).
3. **Ceramiales** (*e.g.*, *Polysiphonia*, *Ceramium*).
4. **Cryptonemiales** (*e.g.*, *Corallina*).

Nemalionales

This order comprises Rhodophyceae in which no tetraspores are developed.* To it belongs most of the simple members of the Red Algae, including several fresh-water species. All the genera belonging to the other orders occur exclusively in the sea. As our example we shall study the life-history of *Batrachospermum*, one of these fresh-water species.

Batrachospermum moniliforme

This species is found quite commonly in fresh water, occuring most plentifully in clear running streams, but usually under shade. Specimens grown in deep water or shade are dark violet or reddish in colour, while those living in shallow water are olive green. This variation in colour is primarily influenced by the intensity of light.

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* The order is peculiar in that meiosis occurs immediately after fertilization, so that there are no diploid plants. The only exception to this in *Galaxaura*, where most species have become diplobiontic (see p. 181).

The thallus is filamentous, freely branched and gelatinous in texture (Fig. 139). The central filament is made up of a single row of large cells,

FIG. 139.—*Batrachospermum moniliforme.* A branch of the living plant, enlarged.

from which whorls of dichotomous lateral filaments are developed at frequent intervals. Growth is by means of a single apical cell, which cuts off cells basipetally by transverse divisions. Immediately behind the growing point these cells, which form the central filament, cut off small lateral cells, four from each central cell, and these form the initials from which the side branches arise. The lateral cells, though actively dividing, remain small themselves, while the cells of the central filament elongate considerably, so that eventually the groups of lateral cells are widely separated and appear to form nodes on the axis. From these nodes grow out the richly branched clusters of side shoots, which give the whole axis that beaded appearance to the naked eye from which the specific name of " moniliforme " is derived.

In addition to the side shoots the cells at each node give rise to filaments which grow longitudinally downwards to the next node, covering the axis cells with a loose mantle or **pseudo-cortex.** Here and there also one of the nodal cells is transformed into an apical cell and gives rise to a secondary long shoot which repeats the structure of the main axis. The cells of the lateral branches contain several irregular plastids, which are termed **chromatophores,** each possessing a single pyrenoid.

SEXUAL REPRODUCTION

The sex organs may be produced on the same or on different plants. The male organ is the **antheridium,** but the female organ is called the **carpogonium** and differs in some respects from the oogonium of the other groups of Algae.

The antheridia are very small, and arise in terminal clusters on the side branches, frequently near the female organs. The side branches produce short antheridial branchlets, on each of which four antheridia are borne. Each antheridium liberates a single naked, non-motile, spherical body which is called a **spermatium.**

The carpogonium develops on a specialized lateral branch, which is called the **procarp** (Fig. 140). It arises near the base of a vegetative branch, and generally consists of a filament of four cells. The terminal cell becomes the carpogonium and soon develops a swelling at its anterior end, which elongates very considerably and forms a filamentous structure known as the **trichogyne.** In some types of Red Algae the nucleus of the carpogonium divides at this stage, and one of the daughter nuclei migrates into the trichogyne, but this does not normally occur in *Batrachospermum*. Meanwhile the carpogonium enlarges, the chromatophore which it originally contained disappears and the female nucleus sinks to the base of the cell.

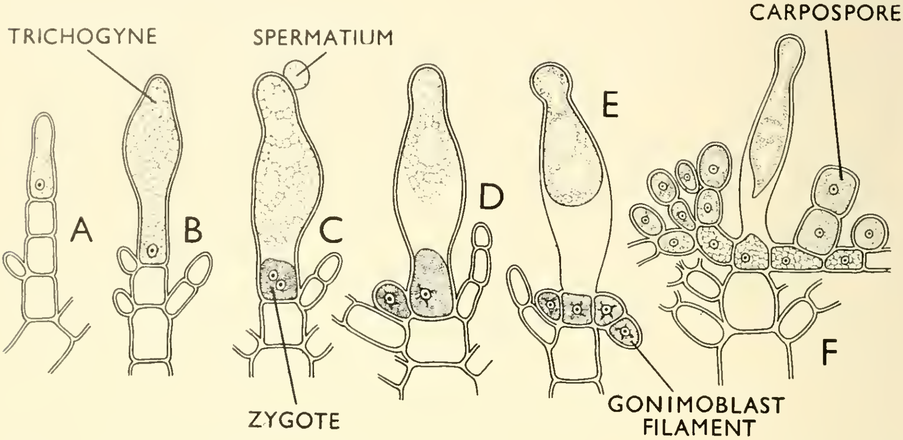

Fig. 140.—*Batrachospermum moniliforme.* A and B, Development of carpogonium. C, Fertilization stage. D, Germination of zygote. E, Beginning of gonimoblast filaments. F, Carpospores forming on gonimoblast filaments. (*After Kylin.*)

Spermatia which have been liberated from the antheridia are carried by the water to the trichogyne, to which they adhere. The wall of the trichogyne breaks down at the point of contact with the spermatium, and the nucleus of the spermatium migrates into it. It then passes down the trichogyne and fuses with the female nucleus in the carpogonium, after which the basal part of the carpogonium is isolated by a cross wall and forms the **zygote.** The zygote nucleus divides into two, one nucleus then migrates into a lateral protrusion which develops in the side of the zygote, and is cut off by a wall. The remaining nucleus then also divides and a second lateral protuberance is formed into which one of the daughter nuclei migrates. From these lateral cells, cut off from the zygote, filaments of cells develop which are called **gonimoblasts.** They branch repeatedly and small spores termed **carpospores** are formed at their ends.

When the carpospores are mature the spore wall bursts and the naked protoplasmic mass escapes, comes to rest, develops a new wall and germinates into a pad or **sole** of parenchymatous tissue, from which develop numerous shoots of a simple filamentous plant. This plant is spoken of as the **Chantransia stage** on account of its resemblance to another Alga of that name. Terminal cells on the lower branches of these filaments function as apical cells, and from them fresh *Batrachospermum* plants arise. They may also arise directly from the sole.

Asexual Reproduction

There are no tetraspores produced in *Batrachospermum*, but **monospores** may be developed on the Chantransia filaments. These arise singly in sporangia borne at the ends of short branches and on liberation give rise to fresh plants of the Chantransia stage.

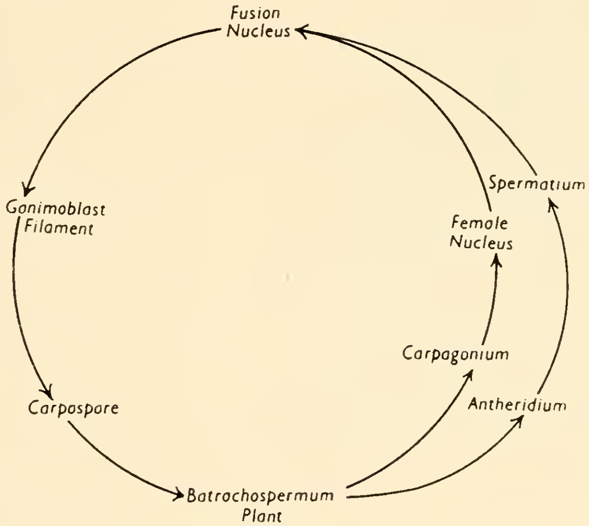

FIG. 141.—Life-cycle of *Batrachospermum*.

Gigartinales

The Gigartinales are Rhodophyceae in which the thallus is usually divisible into a flat frond and an attaching disc, though in certain parasitic genera the structure of the thallus may be greatly reduced. In the majority the thallus is composed of a tissue of much-branched filaments of cells showing considerable morphological differentiation.

In many species the plants are dioecious, though a few are monoecious, but in either case the zygote gives rise to a large tetrasporic plant, morphologically like that of the gametophyte. The sexual reproduction involves the development of a procarp branch and an auxiliary cell is present before fertilization. A fairly extensive carposporophyte tissue may be produced.

Most of the species are free-living, but the group includes two genera, *Harveyella* and *Choreocolax*, which are parasitic on other Rhodophyceae.

We shall consider in detail one example of the group, *Chondrus crispus.*

Chondrus crispus (Irish Moss or Carragheen Moss)

This is the only species of the genus which is found in British waters. It shows considerable variation in the form of the thallus, but is always divisible into a shoot and an attaching organ. It is very plentiful around our coasts, occurring mostly just above low tide mark wherever the shore is rocky.

The **attaching organ** is a flat, not very thick plate of tissue, which adheres very closely to the substratum and anchors the seaweed firmly to its support. In colour it is faintly red, and it may to some extent assist in the assimilation of food, though its primary function, apart from anchorage, is the storage of elaborated food material. It grows by extension of the margin and covers anything which may be attached to the rocks, extending into holes and crevices, thus increasing its hold on the rock surfaces.

Fig. 142.—*Chondrus crispus.* Form of entire plant. Half natural size.

From this attaching organ numerous upright **shoots** are produced (Fig. 142). These are at first undivided and more or less round in section, but after growing to a height of about 3 cm. they begin to expand and to dichotomize into two equal branches, each of which forms a flat frond of varying width and thickness. By successive dichotomies a fan-shaped thallus is produced which may lose its basic regularity of division. The degree of division and the breadth of the segments have been employed as criteria for separation into a number of varieties. These are, however, of little value since they are by no means constant. In general, it may be said that the higher up the beach the plant grows the smaller and narrower the thallus becomes. Similarly the colour of the fronds varies from dark red to pink, and even to greenish-brown if one compares plants near low tide with those nearer high tide mark. Presumably therefore the darker red colour is associated with deeper water and less light, a feature which has already been mentioned in connection with *Batrachospermum.*

Structure of the Shoot

The centre of the shoot is occupied by very much elongated, rather narrow **central cells** with fairly thick walls, which form an interwoven tissue. These cells are united to one another at certain points where the cells narrow and a thin cross-membrane is formed, leaving a tiny pit through which cytoplasm is continuous. On each side of the pit is a small cap, consisting of what appears to be coagulated cytoplasm.

Connecting with these central cells are the **collecting cells.** They are considerably shorter, and in passing towards the periphery of the thallus they get progressively smaller. They are connected together by pits, with or without protoplasmic caps, and form a network around the longitudinally running central cells.

On the periphery of the thallus are the **assimilating cells,** which form rows parallel to one another but curved upwards and outwards at a constant angle to the longitudinal axis of the whole shoot. These cells possess numerous pits which are always destitute of protoplasmic caps.

The whole thallus thus consists of a complex system of long and richly branched filaments of which the assimilating cells form the ultimate branches. Such a tissue is termed a **plectenchyma.** As a general rule division in these filaments takes place at right angles to the longitudinal axis of each cell row.

Growth takes place not only at the apex of the shoot, where cell division is going on rapidly, but growth in width occurs at the apices of the assimilatory cell rows, where new assimilatory cells are cut off terminally, while the basal cells of the assimilatory branch become collecting cells. Growth in length may be produced by the elongation of the central cell, by the enlargement of the conducting cells and by the further branching of the assimilatory filaments to produce new rows among the pre-existing ones.

Structure of the Attaching Organ

The attaching organ does not show the division into separate zones that is found in the shoot. The cells nearest the substratum form a layer of irregularly arranged cells of varying shapes which fit into the minute crevices in the substratum (Fig. 143). They have thick cell walls and form an **attachment layer,** three or four cells thick. The remainder of the attachment is composed of rectangular cells in very regularly arranged rows,

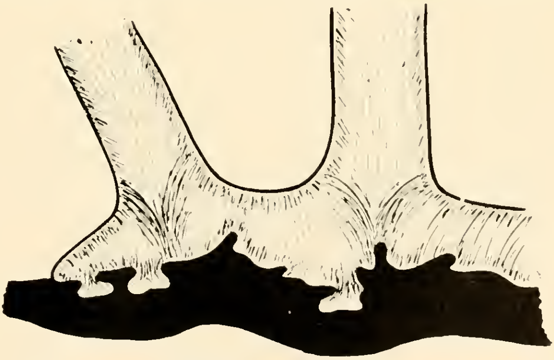

Fig. 143.—*Chondrus crispus.* Holdfast at base of stipe. (*After Darbishire.*)

which run at right angles to the surface of the whole disc. Growth is effected by the formation of fresh rows of cells at the margin.

The cells of the attaching disc, though containing chromoplasts, and therefore capable of assimilation, are primarily storage organs and are packed with flattened, discoid starch grains. These grains give a brown rather than a blue colour with iodine, showing that the chemical constitution of the starch is different from that in higher plants. It is known as **floridean starch.** This starch is also found abundantly in the collecting and conducting filaments of the stem.

Sexual Reproduction

Chondrus shows a clear alternation of generations between sexual and asexual generations, though the plants are morphologically alike. The male and female reproductive organs are borne on separate fronds. It is apparently uncertain whether both types may arise from the same basal attachment, though it is unlikely. The tetrasporic plants occur chiefly in the winter.

The sex organs consist of **antheridia** and **carpogonia.** The antheridia are borne on small, slightly flattened segments in which the chromoplasts are poorly developed so that the segments appear almost white. The female organs are located in the central part of the upper ends of the vegetative fronds, forming raised oval areas 1 to 2 mm. in length. The asexual reproductive organs occur near the apices of the young fronds. They appear as elongated, dark spots, accompanied by slight bulging of the assimilatory layer. Such protruberances of the thallus, in which reproductive organs occur, are termed **nemathecia.**

The Antheridium

The specialized segments of the thallus on which antheridia occur are almost colourless, but their structure differs little from that of the vegetative thallus. It is only the peripheral cells of the assimilatory filaments which are modified. The last two or three cells of each filament are colourless owing to the great reduction in the size of the chromoplasts. These two or three cells constitute the male organ and each cell may be regarded as an antheridium, for it gives rise to a single male gamete or **spermatium** (Fig. 144). This escapes as a colourless round mass of protoplasm devoid of any cell wall or flagella. A fragment of the plastid is present but is not sufficient to colour the gamete. The spermatia are shed from October to December.

The Carpogonium

The development of the female organ in *Chondrus* has not been fully investigated, but so far as is known the process occurs as follows. Certain segments of the upright fronds take on the function of forming the female organs. In the early stage the central conducting tissue consists of slightly elongated, starch-filled elements which are destined to play later an important part in the formation of the reproductive cells. The assimilatory zone then begins to form **procarp branches.** Each procarp consists of four cells. The lowest cell is termed the **basal cell** and is in protoplasmic connection with the collecting cells of the thallus. It is followed by two intermediate cells, and the branch is terminated by the **carpogonium,** which is more or less flask-shaped, with an enlarged basal part containing the female nucleus and an elongated **trichogyne** which projects beyond the outer limit of the assimilatory zone into the water. The spermatium becomes united to the trichogyne, and the male nucleus passes down the trichogyne and presumably fuses with the female nucleus.

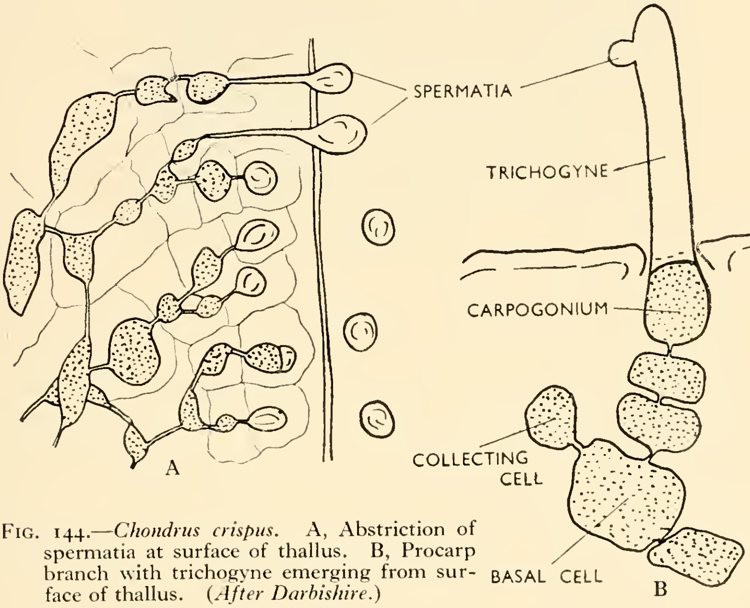

Fig. 144.—*Chondrus crispus.* A, Abstriction of spermatia at surface of thallus. B, Procarp branch with trichogyne emerging from surface of thallus. (*After Darbishire.*)

After fertilization a wall is laid down cutting off the trichogyne which then withers and disappears. The carpogonium now unites with the basal cell which thus functions as the **auxiliary cell,** and the zygote nucleus passes into it.

From the auxiliary cell a number of filaments now begin to develop. These are termed the **gonimoblast filaments** and are characteristic of many Rhodophyceae. They form secondary connections with the neighbouring collecting and conducting cells from whose reserves of starch they draw nourishment. From the tips of the gonimoblast filaments two or three cells are cut off, each of which produces one **carpospore.** These spores are liberated into a cavity (Fig. 145), formed by the collapse of the exhausted cells of the conducting and central filaments, which may be regarded as a **cystocarp,** a term used for any structure enclosing carpospores.

The mature carpospores are roundish bodies which are at first devoid of a cell wall. They possess a very dense cytoplasm with a large amount of starch and are deep red in colour. They are finally liberated and presumably germinate to produce the tetrasporic plants, though the stages in this process have not been followed in detail.

FIG. 145.—*Chondrus crispus.* Nemathecium containing carpospores.

THE TETRASPORANGIUM

The asexual reproductive organs appear on the tetrasporic plants between December and March. The nemathecia may be recognized by holding the frond to the light when they may be seen as elongated dark spots near the tips of the younger fronds.

The internal tissue of the nemathecium contains irregular rows of cells which form protoplasmic connections with the collecting cells and assimilating cells. The cells in these rows gradually enlarge, become filled with starch and are dark red in colour. Each functions as a **tetrasporangium.** At first it is possible to see the regular arrangement of these cells in rows, but as they enlarge still further they become displaced, while the surrounding sterile cells give up their food material and collapse, forming the cavity of the nemathecium, which is filled by the developing tetrasporangia (Fig. 146).

The nucleus of the tetrasporangium now divides into four, during which meiosis occurs, resulting in the formation of four monoploid nuclei. A wall is then laid down across the cell, and in each cell thus separated a further wall is formed, which may be laid down in the same plane or at right angles to the first one. In this way four **tetraspores** are produced in a **cruciate** group. The arrangement in which the tetraspores are produced in the Rhodophyceae is an important point in classification. The tetraspores germinate to produce fresh sexual plants.

Chondrus follows the same general life-cycle as in *Polysiphonia* (see p. 168), in which there is also an alternation of sexual and asexual generations, but with one important difference. As a result of sexual fusion quite an extensive tissue is developed by means of the gonimoblast filaments before the carpospores are produced. This tissue, since it is derived from the fertilized carpogonium, is diploid and is termed the **carposporophyte.** Its existence is terminated by the carpospores, which in turn give rise to diploid **tetrasporophytes.** The reduction division occurs in the formation of the tetraspores which on germination initiate a **gametophyte.** Thus in this Alga, as in many other members of the Rhodophyceae, there is an alternation of not two but three generations.

Fig. 146.—*Chondrus crispus.* Development of tetraspores in tissues at margin of thallus.

The life-cycle of *Chondrus* may, therefore, be represented by the diagram (Fig. 147).

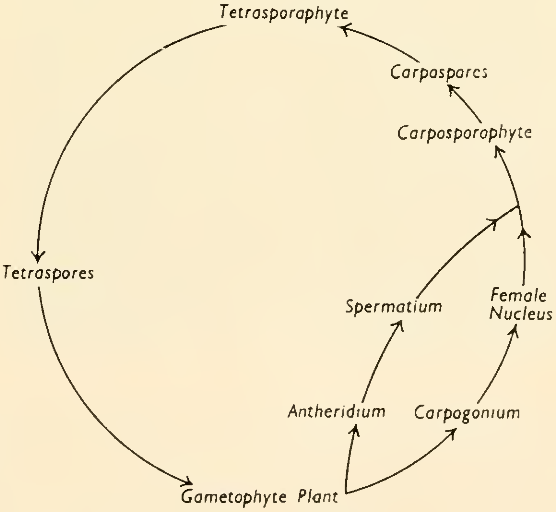

Fig. 147.—Life-cycle of *Chondrus*.

Chondrus crispus is, or used to be, employed in the preparation of jellies as a substitute for gelatine, especially in invalid cookery. In recent years it has also proved to be valuable as a substitute for agar.

Ceramiales

The Ceramiales are Rhodophyceae in which the auxiliary cell is only cut off from the basal cell of the procarp branch *after* fertilization. In many species two auxiliary cells and two procarp branches are cut off, one from each side of the basal cell. The carpospores arise from very short **gonimolobes** derived from the auxiliary cell and consequently the carposporophyte is small. The carpospores are formed in a cluster and are developed on short side branches of the main filaments. They are sometimes enclosed in a **cystocarp.**

There is a diplobiontic alternation of generations (see p. 181) in which the tetrasporic plants are morphologically similar to the gametophytic ones.

The order includes a number of common genera of which *Polysiphonia* is probably the best known in British seas, but other genera are also common, and we may mention *Ceramium* and *Callithamnion* as other members of the order. We shall consider as our types the abundant species *Polysiphonia nigrescens* and *Ceramium rubrum.*

Polysiphonia nigrescens

The thallus of *Polysiphonia* (Fig. 148) looks superficially like a simple branched filament (Fig. 149), but it is actually composed of a system of parallel filaments, termed **siphons.** There is a central siphon composed of relatively large, elongated cells surrounded by a variable number of peripheral or **pericentral** siphons. The number of these varies between four and twenty, but it is fairly constant in each species (Fig. 150).

FIG. 148.—*Polysiphonia fibrillosa.* Habit of growth.

At the extreme apex the thallus consists only of the cells of the central siphon, which originate by the divisions of an **apical cell** (Fig. 151). The pericentral cells are cut off successively from the central cells by a series of tangential longitudinal divisions which begin at one side and continue in both directions round the cells (Fig. 152).

FIG. 149.—*Polysiphonia nigrescens.* Part of vegetative thallus showing dichotomous growth.

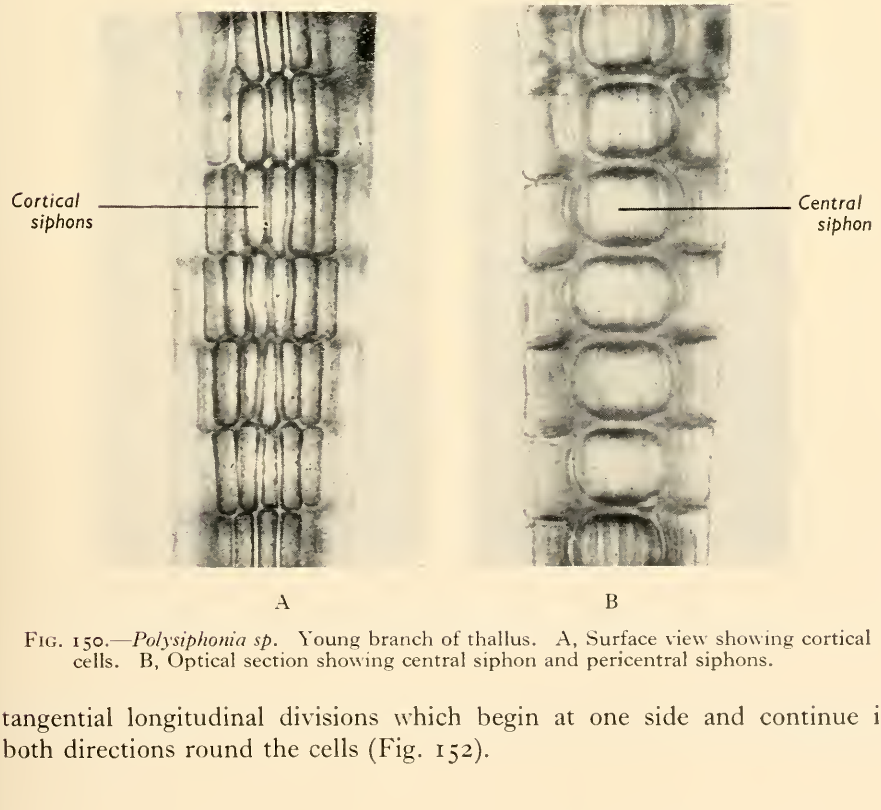

FIG. 150.—*Polysiphonia sp.* Young branch of thallus. A, Surface view showing cortical cells. B, Optical section showing central siphon and pericentral siphons.

The main branches of the thallus are initiated by oblique divisions of the apical cell. Smaller monosiphonous branches of limited growth, called **trichoblasts**, are cut off from the upper ends of certain of the pericentral cells.

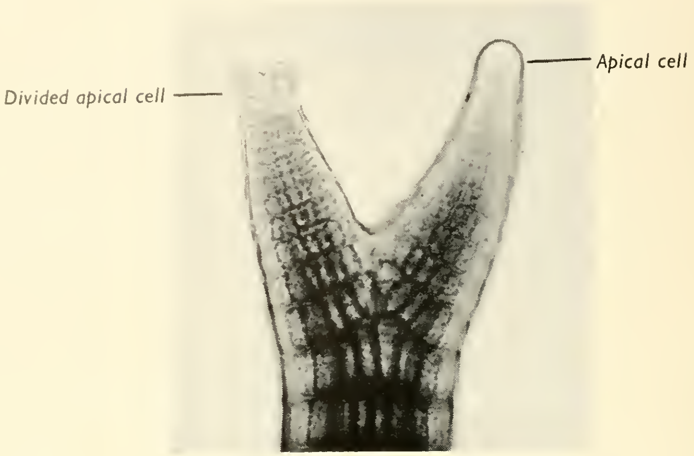

Fig. 151.—*Polysiphonia sp.* Apex of frond showing dichotomy of apical cell.

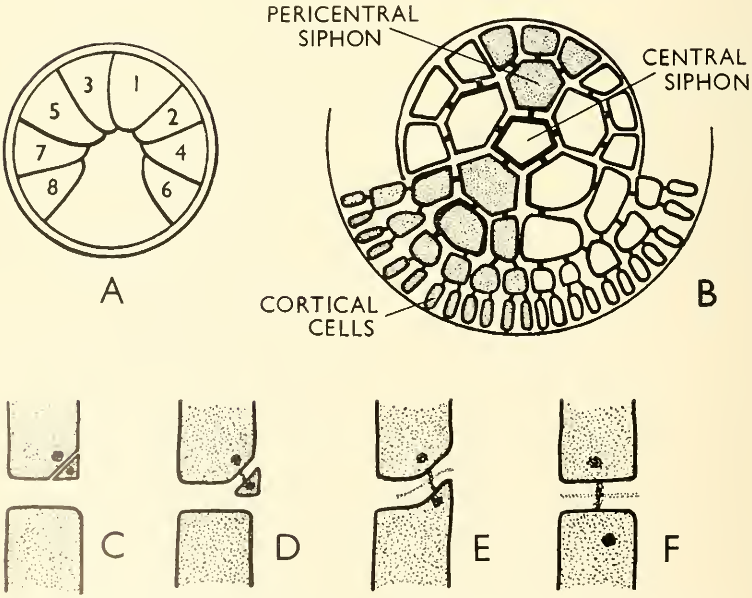

Fig. 152.—*Polysiphonia fastigiata.* A, Formation of pericentral siphons in transverse sequence, cut off from cell of central siphon. B, Transverse section of completed structure of branch. C to F, Development of the connection between two cells of a pericentral siphon.

The cells of the pericentral siphons form regular tiers, each of which is equal in length to the corresponding cell of the central siphon. The thallus thus has the appearance of being divided into nodes and internodes, which is characteristic and distinctive.

The pericentral cells of different tiers are at first unconnected, but connections soon develop by a peculiar method. A small triangular cell is cut off at a lower corner of a pericentral cells but remains connected to its parent cell by a protoplasmic thread. This small cell fuses with the pericentral cell immediately below it, thus establishing a protoplasmic connection between the two tiers (Fig. 152, C to F).

In older branches of the thallus the pericentral cells divide again repeatedly by periclinal walls, cutting off a number of external layers of cells which divide transversely into smaller cells, forming a **cortex.** These cells are all connected together by protoplasmic threads and are comparable to a system of contracted branches, the outermost cells of which form a superficial assimilating layer.

The thallus is attached at the lower end by means of a system of short filaments or **rhizoids,** whose distal ends are swollen into attaching discs fixed to the rock.

Polysiphonia grows quite commonly around the British coasts below high tide mark, both on rocks and in pools. In colour it varies from clear red to purple. One common species, *Polysiphonia fastigiata*, lives as a semi-parasite on the Brown Seaweed, *Ascophyllum nodosum.* We have here an example of an Alga which may be in process of becoming a parasite, for *Polysiphonia fastigiata* can still live an independent life, though it has been shown that plants living apart from the host are smaller and less healthy than those which are attached to *Ascophyllum.*

SEXUAL REPRODUCTION

In *Polysiphonia* male, female and asexual reproductive organs are all borne on separate plants which are morphologically identical.

THE ANTHERIDIUM

The **antheridia** arise on short branches which are formed in clusters near the tips of the main filaments (Fig. 153). Each antheridial branch consists of a central trichoblast filament, which cuts off laterally a number of pericentral cells, each of which further cuts off a number of **antheridial mother cells,** from each of which are formed three or four **antheridial cells.** From the latter **spermatia** are liberated. The central filament is quite covered and hidden by the mass of colourless spermatia (Fig. 154).

THE CARPOGONIUM

The **procarp** consists of a row of three or four cells arising from a pericentral cell. The last cell of the branch enlarges and a thin terminal portion grows out to form the **trichogyne**, while the lower part of the cell enlarges as the **carpogonium**.

FIG. 153.—*Polysiphonia fastigiata.* Branches bearing antheridia.

The spermatia are borne passively to the trichogyne and the male nucleus enters and passes down it, finally fusing with the carpogonial nucleus, which lies at the base of the carpogonium. Then the trichogyne shrivels up and disappears.

The processes which follow fertilization are complex and differ considerably in different species. We will first take as a type one of the simpler examples, *Polysiphonia nigresceus*, which is a common British species.

The basal cell of the procarp branch, which is known as the **supporting cell,** cuts off upwards a new cell which is called the **auxiliary cell** (Fig. 155). This cell becomes attached to the carpogonium by a wide protoplasmic connection. The fertilized diploid nucleus of the carpogonium now divides and one of the daughter nuclei passes over into the auxiliary cell. A wall is formed cutting it off from the carpogonium, which later withers.

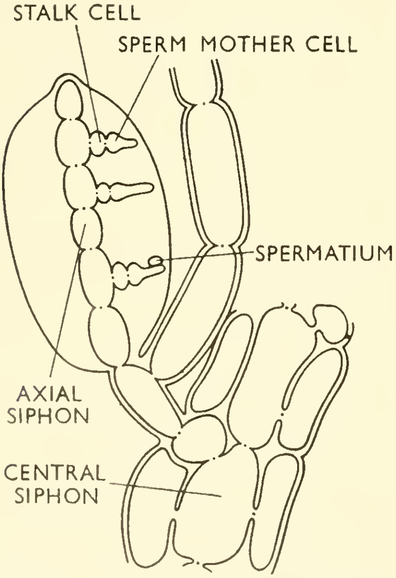

FIG. 154.—*Polysiphonia violacea.* Structure of the antheridial branch. (*After Yamanouchi.*)

In the auxiliary cell there is already its own monoploid nucleus, which, however, soon disappears. The diploid nucleus from the carpogonium divides and one nucleus enters a branch of the auxiliary cell, which becomes the primary cell of a **gonimoblast.**

The auxiliary cell also fuses with the supporting cell of the procarp, and both fuse with the pericentral cell of the vegetative axis, forming a complex called the **central cell,** which apparently only provides nourishment for the developing gonimoblast, since no nuclear fusions occur.

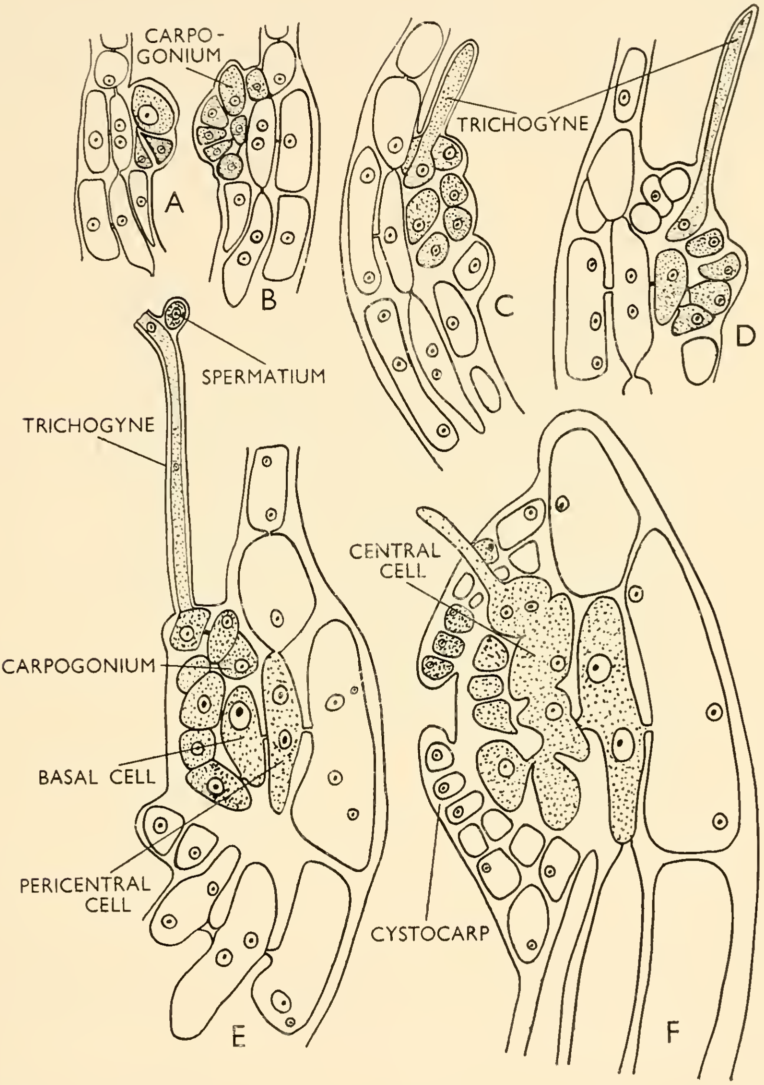

Fig. 155.—*Polysiphonia nigrescens.* A, Initial of the procarp branch. B, Separation of the carpogonium. C and D, Development of the trichogyne. E, Fertilization stage. F, Formation of the central cell of the carposporophyte. (*After Kylin.*)

From the primary cell of the gonimoblast other cells grow out, which in turn bear the **carpospores.** The latter when liberated germinate to produce asexual plants or sporophytes. Fifty to sixty carpospores may be formed.

In *Polysiphonia violacea*, another species which has been fully investigated, the development of the procarp branch after fertilization is somewhat more complex (Fig. 156). Instead of a single auxiliary cell, a number are formed, and these are produced, not from the basal cell of the procarp branch but from the pericentral cell. This cell cuts off two cells, one of which divides once again ; the other produces a cluster of five cells, which lie beside the carpogonial branch. The end cell of the group (*a*.3) lies between the carpogonium and the pericentral cell.

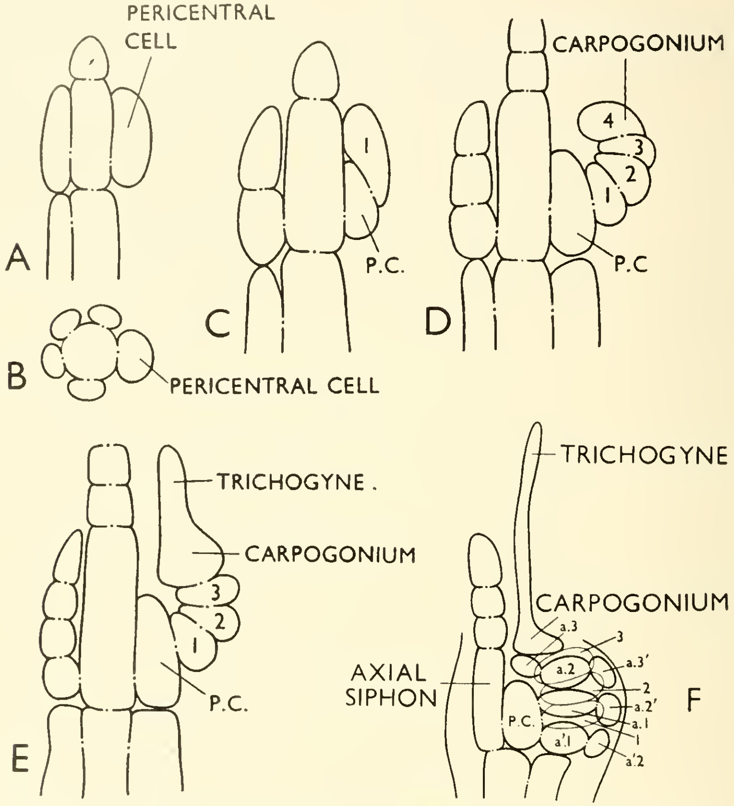

Fig. 156.—*Polysiphonia violacea.* A to E, Stages in the development of the procarp branch. B, Transverse section. F, Formation of auxiliary cells. (*After Yamanouchi.*)

The fertilized nucleus in the carpogonium divides, and meanwhile cytoplasm from the cells of the procarp branch passes into the carpogonium, presumably as nourishment. A wide protoplasmic connection now develops between the carpogonium and the auxiliary cell (*a*.3) which in turn becomes united with the pericentral cell. Through the channel thus formed the two diploid nuclei from the carpogonium pass into the pericentral cell. The carpogonium and the cells of the procarp branch now disorganize. The auxiliary cells next draw closer together, and wide protoplasmic connections becomes established between them and also with the pericentral cell. This general cell-union finally results in the formation of a large irregular central cell. This cell therefore contains the two diploid nuclei and the disorganizing monoploid nuclei of the component auxiliary cells.

The diploid nuclei now divide repeatedly and lobes (**gonimolobes**) are formed on the surface of the central cell. Into each of these a diploid nucleus passes and divides, a cross wall being formed to separate a stalk cell from a terminal carpospore.

In each species while this development has been going on, an envelope has grown up from the peripheral siphons of the axis, which completely encloses the whole of the female organ and later the carpospores. This structure is swollen and urn-shaped, and it, together with the reproductive organs within, is termed the **cystocarp** (Fig. 157).

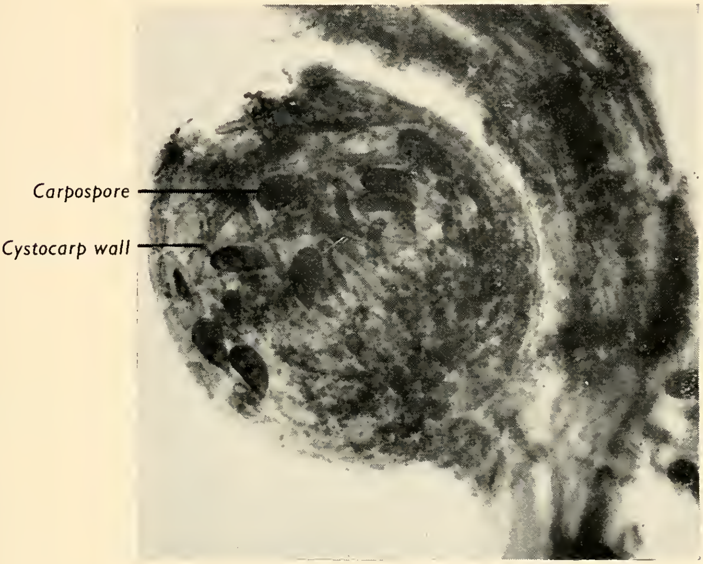

Fig. 157.—*Polysiphonia sp.* Mature cystocarp attached to branch showing contained carpospores.

Asexual Reproduction

On liberation, the carpospores give rise to plants exactly like the parents, but on which asexual spores arise from the pericentral cells of the young branches (Fig. 158). Only one pericentral cell in each tier is fertile. It divides longitudinally by a tangential wall, and the inner half then divides horizontally to produce a lower stalk cell and an upper cell which becomes the **tetrasporangium.** Its protoplast divides tetrahedrally into four **tetraspores,** and it is here that meiosis occurs, so that the spores and the sexual plants which they subsequently produce are monoploid (Fig. 159).

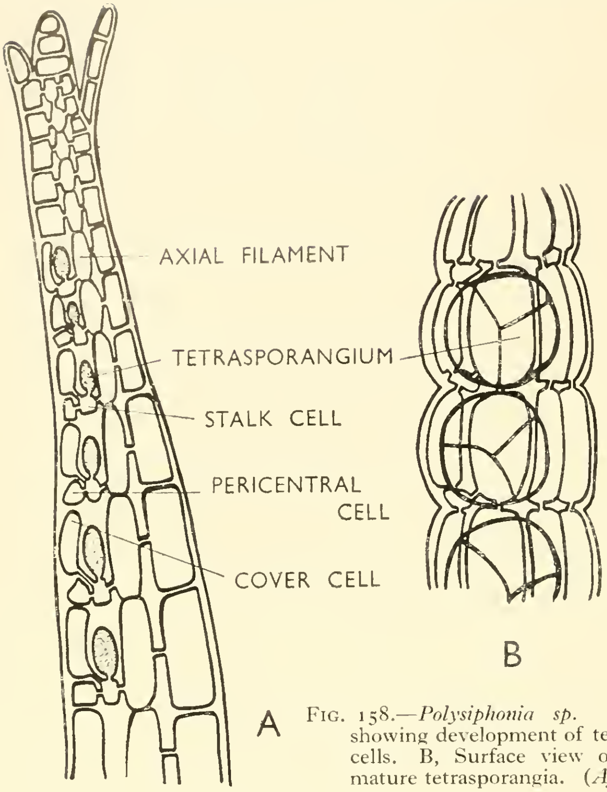

Fig. 158.—*Polysiphonia sp.* A, Tetrasporangial branch, showing development of tetrasporangia from pericentral cells. B, Surface view of an older branch showing mature tetrasporangia. (*After Smith.*)

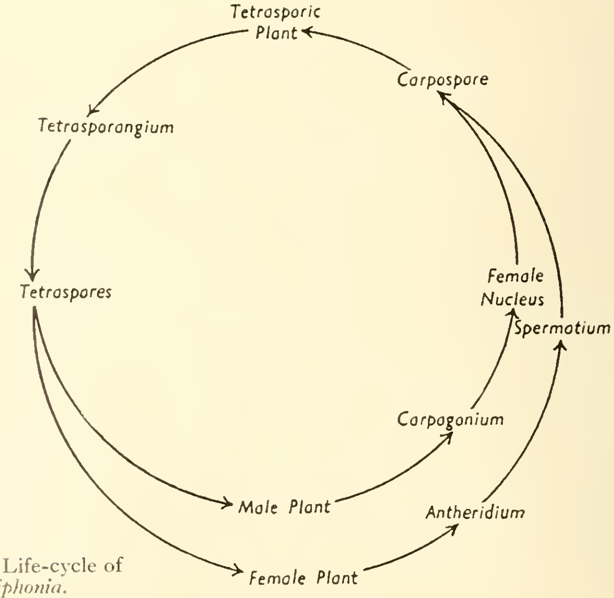

Fig. 159.—Life-cycle of *Polysiphonia.*

Ceramium rubrum

This plant is among the commonest of all the British marine Algae, occurring all round our coasts, chiefly in rock pools of the midshore zone, attached to rocks, stones or to other Algae. The plants can be recognized under a hand lens by the incurved (connivent) tips of the apices of the filaments (Fig. 160). The plants usually grow in tufts, varying from 2 to as much as 30 cm. in length, and rather irregularly dichotomously branched. The fronds are clear red in colour when living in deep sea, or reddish brown or yellowish green when living in shallow tidal water.

FIG. 160.—*Ceramium diaphanum.* Portion of a thallus, natural size, showing beaded appearance due to incomplete cortication of the central siphon.

The plants are apparently dioecious, the antheridia being formed in sessile patches on the upper branches of the male plants, while the cystocarps are formed at the nodes of the females. The asexual plants resemble the sexual ones, the tetrasporangia being developed in cells of the cortex.

STRUCTURE OF THE THALLUS

The apex of each filament is formed of a single apical cell which cuts off segments basally. Branching begins by the formation of two obliquely intersecting walls in the apical cell, each segment thus cut off becoming the apex of a new branch. This oblique division of the apical cell usually occurs after about a dozen axis segments have been formed, and the further elongation of the axis is due to the expansion of these cells. Before elongation the branches have a characteristic incurved form, and each elongating branch is crowned with a pair of "horns," which are the beginnings of the next youngest branches (Fig. 161).

Fig. 161.—*Ceramium rubrum.* Apices of branches, showing apical dichotomy and appearance of nodes and internodes.

The segments cut off basally from the apical cell become the **central cells** of the axis. Each of these very soon cuts off a single layer of small **pericentral cells,** usually seven in number, beginning on the outer (convex) side of the curved filament and proceeding regularly round to the opposite side. These cells are cut off at the upper end of each central cell so that they form nodal rings (Fig. 162). Each pericentral cell now produces four **cortical cells** which develop and divide, forming a close external layer of irregularly shaped cells around the node. As the cortex is forming the central cells elongate and increase in thickness. In *C. rubrum* the cortical cells divide rapidly enough to keep pace with this growth, so that the filament retains a continuous cortex when mature. In some other species, however, the central cells elongate to such an extent that they separate the nodal bands of cortex from each other, and the equatorial belt of each central cell is left uncovered and exposed.

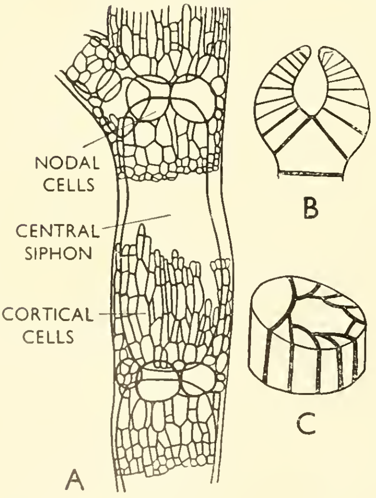

Fig. 162.—*Ceramium areschougii.* A, Development of cortical cells from the nodes of the axis. B, Diagram of apical growth. C, Scheme of the successive development of the pericentral cells. (*From Oltmanns.*)

The outer surface of the cortex is covered by gelatinous material, and at certain seasons there are produced, from the cortical cells, large numbers of long unicellular hairs. In some species, though not in *C. rubrum*, spines may also be developed at the nodes in connection with the primary cortical cells. These spines consist of tapering filaments of about four or five cells. Secondary spines may be developed above and below the primary spines. These consist of only about two cells, and project upwards and downwards at an angle with the cortex.

The organ of attachment in *C. rubrum* develops from the basal cell of the germinating tetraspore or zygote respectively, which elongates and then divides to form a number of rhizoids, each of which becomes multicellular, and forms a flat plate of tissue by means of which the plant is firmly fixed to the substratum of rock. Frequently a number of separate shoots arise from a common basal attachment.

Sexual Reproduction

The sex organs are developed on different plants. The female sex organs are developed terminally on short lateral branches. The groups of carpospores are partly protected by a number of short branches which are formed laterally and grow up to surround, at least partially, the carpospores. No cystocarp envelope is formed. The antheridia are not produced on special organs but are scattered in patches over the surface of the thallus.

The Antheridium

The antheridia arise by the division of cortical cells. In the younger regions every cortical cell may function, but in the older parts of the thallus antheridia formation is limited to the cortical cells of the nodes. Each cortical cell divides first by the formation of periclinal walls and then by anticlinal ones, thus cutting up the cell into four or five cells, each of which functions as an **antheridium mother cell.** This cell next elongates and forces its terminal part through the gelatinous covering, forming a protuberance which is gradually abstricted at its base. This is the **antheridium** (Fig. 163). It is enclosed in a rather thick gelatinous wall which increases greatly in thickness at the apex. The antheridium itself contains a single nucleus enclosed in rather dense cytoplasm. A split occurs in the apex of the antheridial wall and a single **spermatium** slips out.

Meanwhile a projection of the antheridial mother cell grows out and forms a second antheridium, and before the discharge of the second spermatium a third projection may arise. This process appears capable of successive repetitions, until after the production of about six spermatia the mother cell becomes exhausted.

The spermatium contains a single nucleus ; it is oval, and the blunt apex is occupied by the nucleus while the rest is largely filled with vacuolate cytoplasm. It is enclosed in a delicate wall.

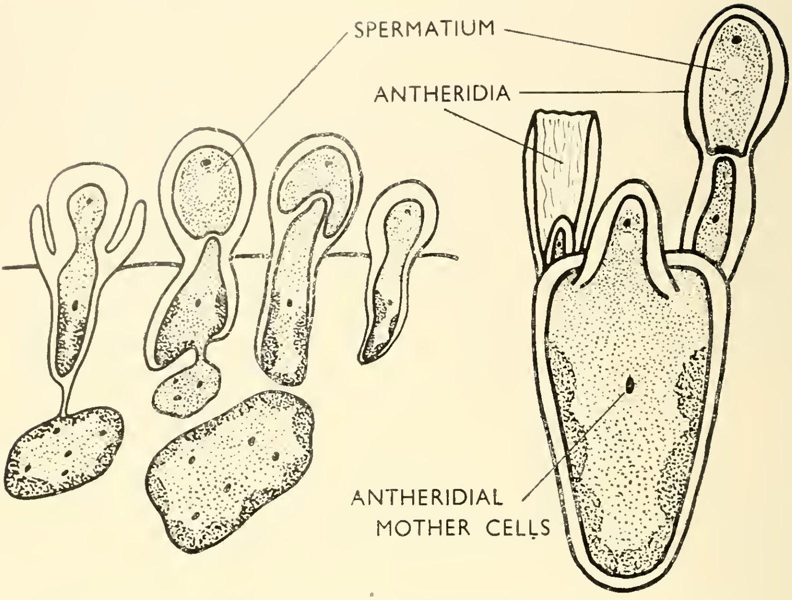

Fig. 163.—*Ceramium rubrum.* Formation of antheridia and spermatia from mother cell. (*Modified from Grubb.*)

The Carpogonium

The **procarp** originates very close to the apex itself. One of the segments cut off by the apical cell divides to form a group of pericentral cells. The first of these to be formed is the initial of the procarp branch. It elongates laterally and becomes the **basal cell.** This cell cuts off a four-celled procarp branch, the terminal cell of which is the **carpogonium.** In *Ceramium rubrum,* unlike other species of *Ceramium,* only one procarp is cut off, either to right or left of the basal cell ; in others two procarp branches are formed. The carpogonium elongates and forms a tubular **trichogyne** at its distal end (Fig. 164). After fertilization the basal cell cuts off on the opposite side to the procarp branch a large **auxiliary cell.** The zygote nucleus from the carpogonium passes into this and the cell then begins to cut off a series of short **gonimoblast filaments,** from the tips of which **carpospores** are formed (Fig. 165). These filaments are often simply short lobes of the auxiliary cell. The carpospores germinate to produce the tetrasporic plants.

Asexual Reproduction

The tetrasporic plants do not differ morphologically from the sexual ones. The **tetrasporangia** arise in the cortical cells in the region of the nodes. The details of the division have not been fully investigated, but it appears probable that they are formed by the division of certain of the pericentral cells in the nodal region, which each cut off externally a single cell which enlarges and pushes between the cortical cells. Not all the pericentral cells at the same level behave similarly, but it is quite common to find transverse bands of from four to about six tetrasporangia formed together at one node. Successive nodes generally behave similarly so that tetrasporangia occur in tiers on the branches (Fig. 166). The nucleus of each **tetraspore mother cell** divides twice, during which meiosis occurs, resulting in the formation of four monoploid nuclei which become arranged around the periphery of the cell. Wall formation is effected by the ingrowth of partitions from the margin, forming four **tetraspores,** but the orientation of the walls varies somewhat, both tetrahedral and cruciate arrangements occurring.

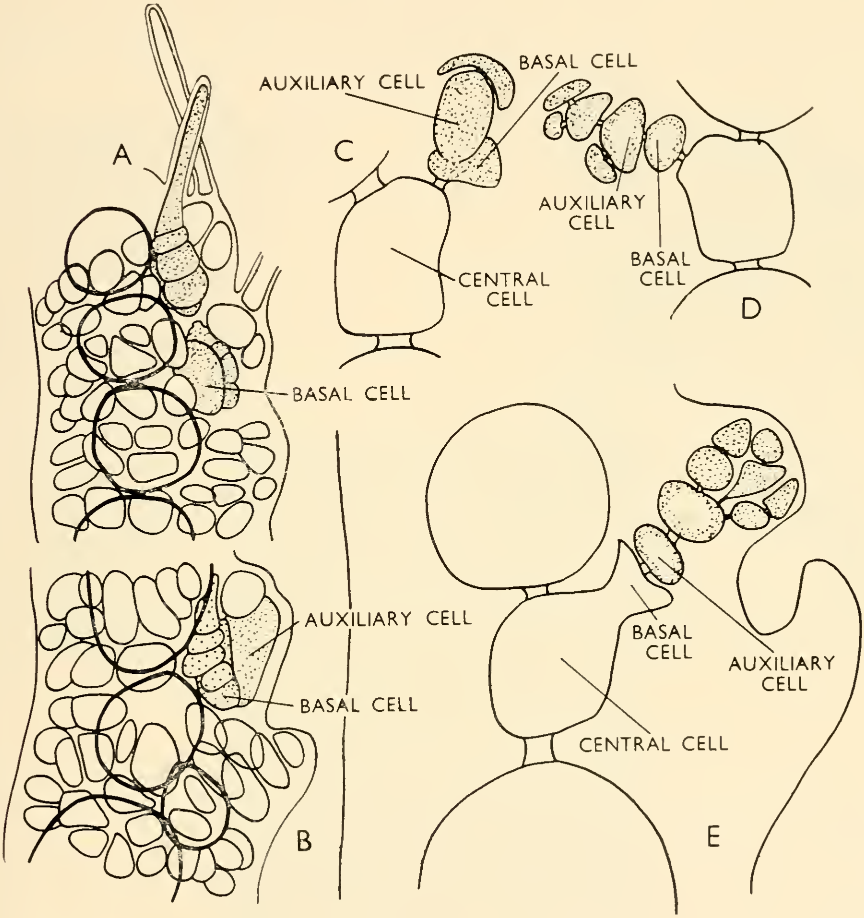

FIG. 164.—*Ceramium rubrum.* A, Procarp branch with trichogyne, on young axis of thallus. Part of a second procarp appears below. B, Procarp after the separation of the auxiliary cell. C to E, Young stages in the development of the gonimoblasts from the auxiliary cell. (*After Kylin.*)

Paraspores are formed in some species, though not in *Ceramium rubrum.* They arise from undivided superficial cells of the cortex and are only formed on the tetrasporic plants. Their germination has not been followed.

The tetraspores are liberated through the gelatinous covering of the thallus as oval bodies which, on reaching a suitable rocky substratum, divide into two cells. The lower or basal cell elongates and forms a rhizoid, whose terminal extremity becomes thickened and flattened and develops into a tiny adhesive disc. The upper cell functions as an apical cell, cutting off a row of cells which forms the central axis of the new sexual plant.

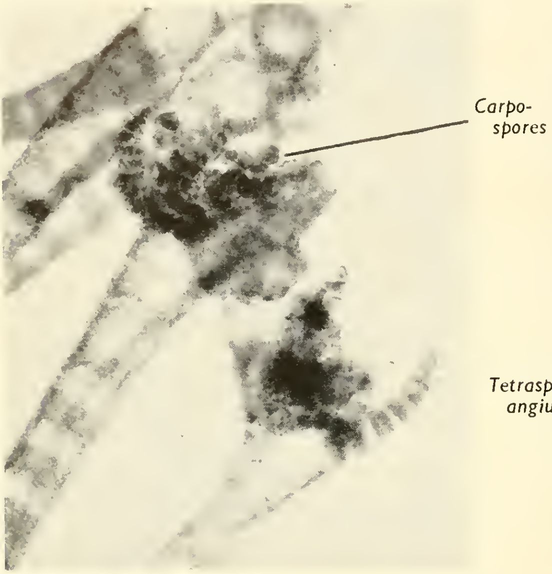

Fig. 165.—*Ceramium rubrum.* Cystocarp with carpospores.

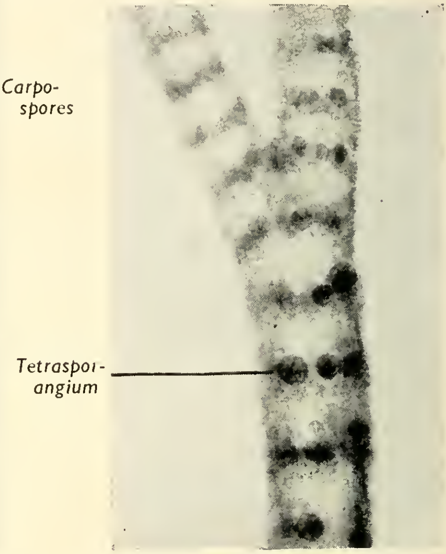

Fig. 166.—*Ceramium rubrum.* Branch with embedded tetrasporangia.

Ceramium rubrum therefore shows the same diplobiontic alternation of generations, as we have seen in other members of the Rhodophyceae (see *Polysiphonia*, p. 168).

Cryptonemiales

The Cryptonemiales are Rhodophyceae in which there are definite unions formed between the auxiliary cells and the cells of the vegetative thallus, which not only serve for nourishment but also form the starting points of the gonimoblast filaments. The result is, in many genera, that an elaborate carposporophyte tissue develops within the tissues of the gametophyte, and the carpospores which arise from the gonimoblasts may be located at positions remote from the procarp branch. The auxiliary cells develop on special filaments *before* fertilization and are actively associated with the post-fertilization changes.

The plants show a diplobiontic alternation of generations and have the most elaborate carposporophytes found in the Rhodophyceae, though the type *Corallina*, which we shall consider in detail, is not the most highly developed genus in this respect.

Many of the Cryptonemiales have their cell walls impregnated with lime. In some the original filamentous character of the thallus is retained, but in others the whole thallus becomes so encrusted in lime that the plant appears to be petrified and forms an amorphous mass resembling coral. Such calcareous Algae do indeed contribute appreciably to the building up of coral reefs. The genus *Lithothamnion* is particularly important in this respect.

As a type of this Order we shall consider the common calcareous Alga, *Corallino officinalis.*

Corallina officinalis

This species occurs very commonly on British shores between tide marks. It is found especially in rock pools, where its small, reddish, jointed tufts are very characteristic (Fig. 167) The colour of the plants varies according to the depth of water in which it is growing. In very deep water it is dull purple, becoming pink and finally white with increasing exposure. The plants are small, rarely more than 9 cm. high, with a basal disc from which the pinnately branched segmented axes arise. These axes are made

Fig. 167.—*Corallina officinalis.* Habit of growth of the plant. Natural size.

up of a series of articulated, multifilamentous segments and are densely encrusted with lime. The segments at the base of the main branches are about as long as broad, but are narrower in the upper parts.

The plants are dioecious, the male and female plants being morphologically alike. As a result of fertilization a tetrasporic plant is developed which again is identical in form with the sexual plants. The reproductive organs are developed in **conceptacles,** those bearing the male organs being pear-shaped, while those producing the female and the asexual reproductive organs are both ovoid.

Structure of the Thallus

The structure of the vegetative thallus is very elaborate and is an example of the **fountain type** of construction. The central part of the thallus is composed of parallel rows of very narrow elongated cells, with numerous lateral branches composed of small cells which are compacted to form a cortex. These cortical cells are filled with dense cytoplasm and chromoplasts, while the cells of the central region are only sparsely provided with cytoplasm.

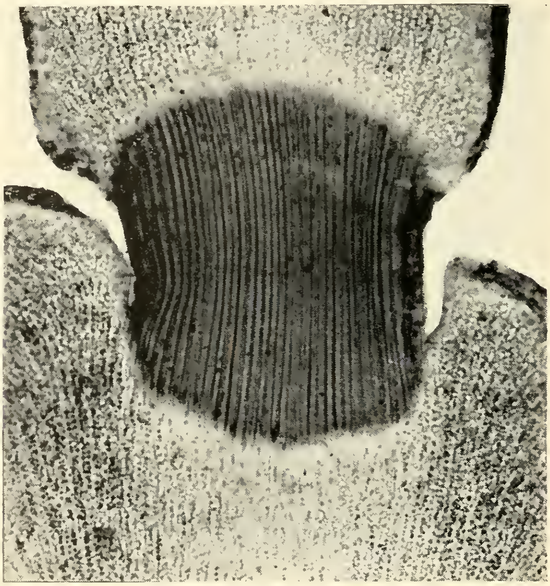

Fig. 168.—*Corallina officinalis.* Structure of the joint between two thallus segments.

The development of a new segment is brought about by the elongation of the axial cells at the apex of an existing segment to form three outgrowths, each consisting of a bundle of narrow cells similar to and continuous with those of the central tissue. These elongated cells divide transversely, cutting off a group of long basal cells which thicken up to form the joint between the segments (Fig. 168) and a series of smaller distal cells which cut off laterally cells to form the new cortex. No cortex is formed on the joint cells.

Growth may therefore be said to be apical, and the cells at the apices of the terminal segments are thin-walled and delicate. It is only further back that the encrustation of lime forms by deposition on the cortical cells. As there is no cortex at the joints they remain uncalcified. This deposit is due to the abstraction of Carbon dioxide from solution in the sea water during photosynthesis, which leads to the dissociation of the Calcium bicarbonate in solution and the deposition of insoluble Calcium carbonate on the surface of the plant. Non-calcified Algae apparently escape encrustation by the continuous sloughing of mucilage from the surface.

As a general rule there are three growing points on each terminal segment; the central one, which continues the growth of the shoot, producing fresh segments, and one formed on each side, which may develop into reproductive organs or may give rise to two lateral branches.

Sexual Reproduction

Whether the conceptacle is destined to contain antheridia, carpogonia or even tetrasporangia, its development is similar, though as we have seen the final shape is somewhat different. Development begins at the apex of a branch. A group of cells at the apex of the growing segment are richly supplied with cytoplasm. These cells are termed the **disc cells,** and those lying at the periphery continue to divide and grow up around the reproductive organs, which develop at the centre of the disc, leaving only a small **ostiole** at the apex and enclosing these organs in a well-formed **conceptacle.**

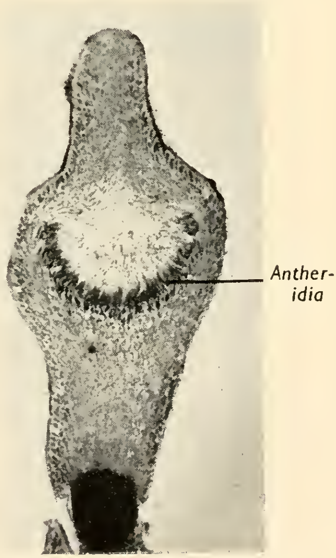

Fig. 169.—*Corallina officinalis.* Longitudinal section of an antheridial conceptacle.

The Antheridium

In the formation of the **antheridia** each disc cell divides into two unequal parts by a wall which cuts off a small terminal cell, which is the **antheridial mother cell.** From this, antheridia arise in twos or threes, forming a close layer over the base of the conceptacle (Fig. 169). These antheridial cells now elongate, and their cytoplasm and nuclei migrate to their upper ends leaving the basal part as a long thin tail. These structures become detached from the mother cells and apparently function as **spermatia,** but their exact nature is uncertain (Fig. 170).

The spermatium has a thin cellulose wall and may therefore be regarded as an antheridium containing one antherozoid, the whole being shed at the same time.

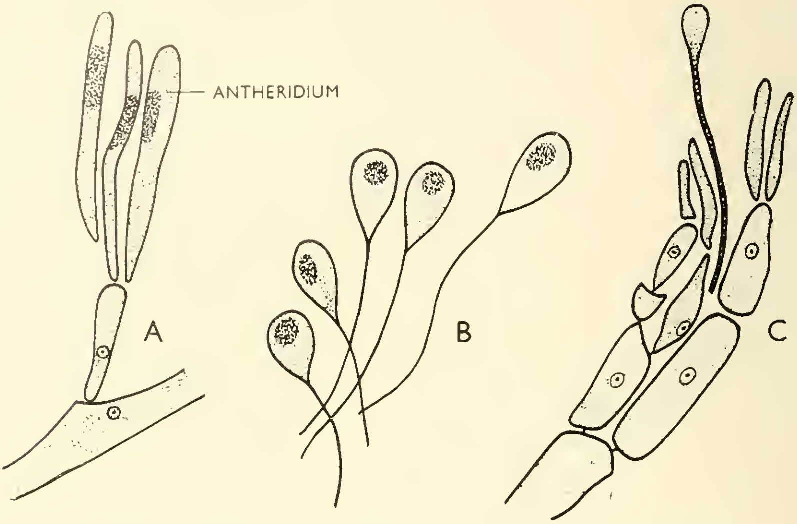

Fig. 170.—*Corallina officinalis*. Formation and liberation of antheridia. A, Antheridia attached to mother cell. B, Free antheridia. C, Mother cells with attached antheridia and one in process of liberation. (*After Sumeson.*)

The Carpogonium

Each disc cell produces a separate **procarp branch.** The cell first divides into two to form an upper cell, which becomes the **auxiliary cell,** and a lower one, which is the **stalk cell.** Then the auxiliary cell gives rise to two sister cells, which are produced side by side (Fig. 171). They are not, however, produced simultaneously, and one has enlarged considerably before the other is produced. The older one enlarges and becomes the **carpogonium,** whose distal end becomes very greatly elongated to form a **trichogyne,** which protrudes through the ostiole of the conceptacle. Meanwhile the nucleus of this cell has divided into two. One remains at the base in the carpogonium, while the other migrates into the trichogyne. The sister cell soon ceases to grow and remains as a small non-functional structure beside the carpogonium. Since all the disc cells within the conceptacle form procarp branches it follows that a large number of separate carpogonia will be formed and that many trichogynes will protrude through the ostiole (Fig. 172).

In this position they are exposed to the sea water and readily catch any spermatia which come into contact with them. Though the point has not yet been definitely proved it is assumed that after liberation from the male conceptacle the spermatium loses its wall, and at the time it comes into contact with the trichogyne it is a naked spherical protoplasmic mass. The nucleus in the trichogyne disorganizes, and the male nucleus migrates down the trichogyne and fuses with the carpogonial nucleus.

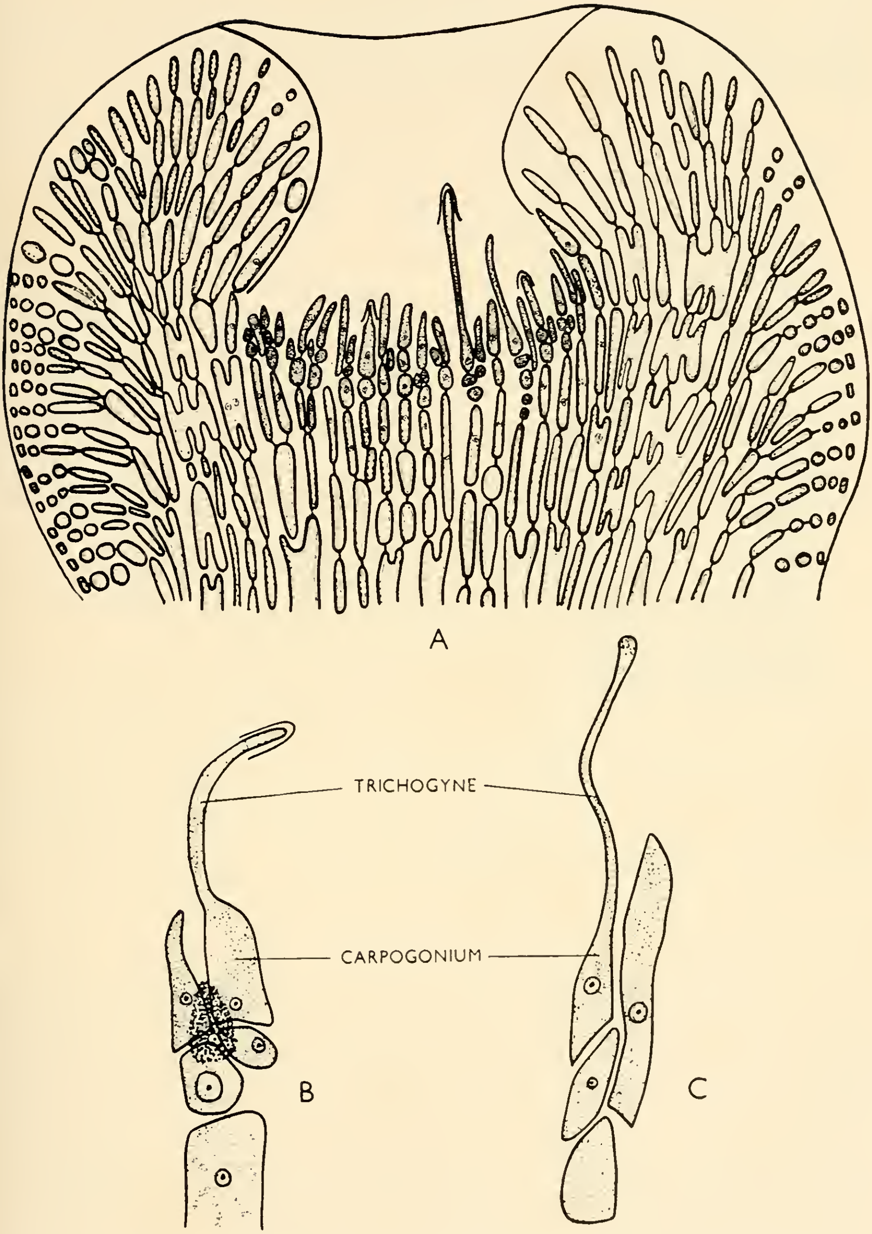

FIG. 171.—*Corallina officinalis*. A, Longitudinal section of a female conceptacle with young procarps. B and C, Young procarps with carpogonia. (*After Sumeson*.)

At this stage the auxiliary cell of this procarp branch fuses with the auxiliary cells of the neighbouring procarp branches until finally a single large **central cell** is produced from the union of auxiliary cells. The diploid zygote nucleus now migrates into the central cell, which thus contains many monoploid nuclei from the auxiliary cells which have contributed to its formation and the diploid nuclei from the fertilized carpogonia. Since many trichogynes may be involved and many simultaneous fusions have occurred there may be as many as a hundred diploid nuclei from different carpogonia.

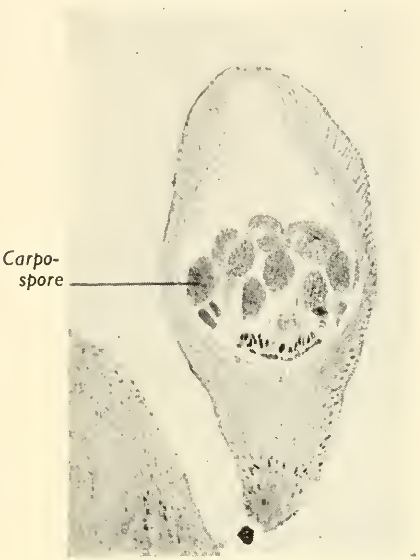

Fig. 172.—*Corallina officinalis.* Longitudinal section of a mature female conceptacle with carpospores.

The monoploid nuclei disintegrate, while the diploid nuclei migrate to the periphery of the central cell, where each divides into two. A lobe appears on the central cell at each of these points, and one daughter nucleus enters it and the tip of the lobe is cut off as a cell. The other nucleus remains in the central cell. This process may be repeated so that chains of cells are cut off in basipetal succession, the number of chains being ultimately dependent on the number of carpogonia which were fertilized. These cells enlarge and become spherical, and are finally constricted off as separate **carpospores.** They separate and escape through the ostiole of the female conceptacle.

The carpospores germinate within twenty-four hours and give rise to new plants identical in structure with the parents, but the nuclei contain the diploid instead of the monoploid chromosome number. These are the plants which will ultimately produce tetraspores and are therefore sporophytic plants.

Asexual Reproduction

The disc cells of the developing asexual conceptacles divide into two, the lower half forming a stalk cell, while the upper becomes the **tetraspore mother cell.** This latter cell grows and assumes a clavate form. Its nucleus enlarges and undergoes two divisions during which meiosis occurs. This reduction division takes place at about the time when the conceptacle has been completely developed. Wall formation follows meiosis. These walls are laid down one above the other so that a row of four **tetraspores** is produced. Such a method of septation is said to be **zonate** (Fig. 173).

The tetraspores are liberated through the ostiole of the conceptacle and float about freely in the water (Fig. 174). They become attached to a suitable substratum, such as a rock face, and germinate, giving rise to sexual plants again.

The life-cycle of *Corallina* therefore shows an alternation of generations between gametophytes, carposporophytes and tetrasporophytes as in *Polysiphonia*, *Chondrus* and *Ceramium*, though there is only a relatively simple carposporophyte, compared with other members of the Cryptonemiales.

ALTERNATION OF GENERATIONS IN THE RHODOPHYCEAE

In the Algae the life history may include only one type of vegetative plant, or there may be two separate kinds of vegetative plants, the one producing gametes and the other producing non-sexual spores or zoospores. In the latter case the plants may be morphologically identical or they may be different in form, sometimes so much so that they were once considered to belong to distinct genera, as in *Cutleria*.

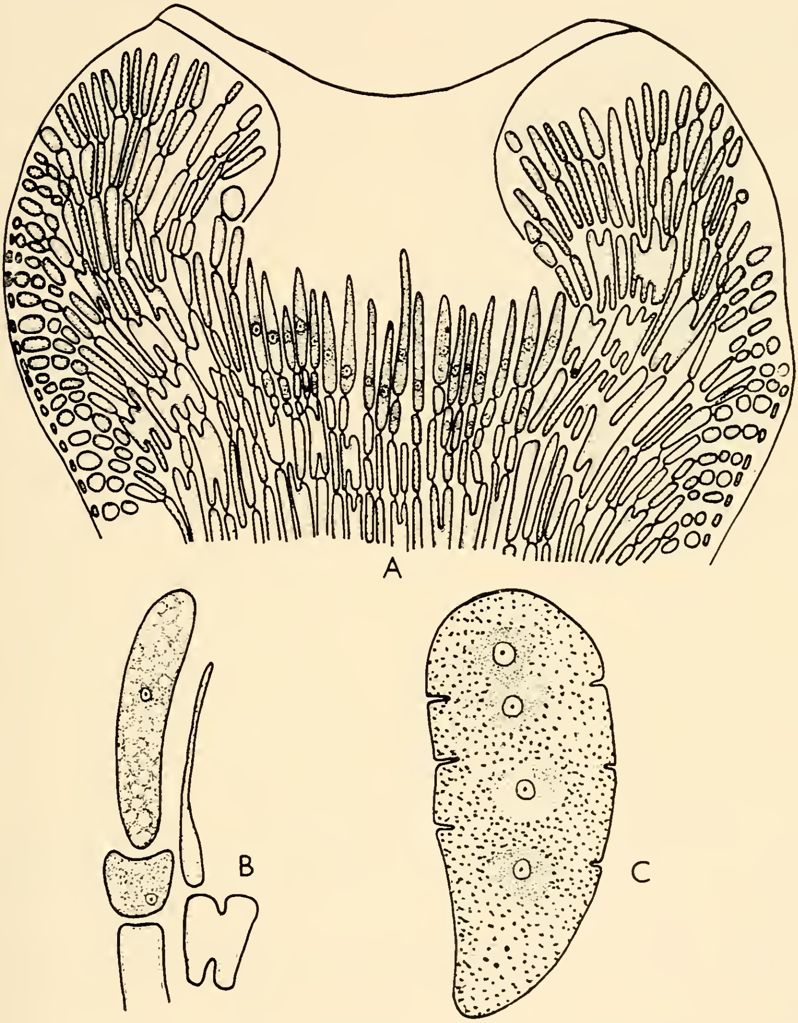

FIG. 173.—*Corallina officinalis*. A, Longitudinal section of a young tetrasporangial conceptacle with young sporangia, not yet transversely divided. B, Young tetrasporangium before meiosis, showing stalk cell. On the right a sporangial rudiment. C, Tetrasporangium in division after meiosis. (*After Suneson.*)

A life-history of the first category, in which there is only one type of vegetative plant, is said to be **haplobiontic**. Examples of this are *Chlamy-*

domonas, *Spirogyra*, *Fucus* and *Batrachospermum*. A life history of the second category which includes two vegetative plants, whether they are alike or not, is called **diplobiontic.** Examples of this are *Cladophora*, *Coleochaete*, *Dictyota*, *Laminaria*, *Cutleria* and *Polysiphonia* (Fig. 175).

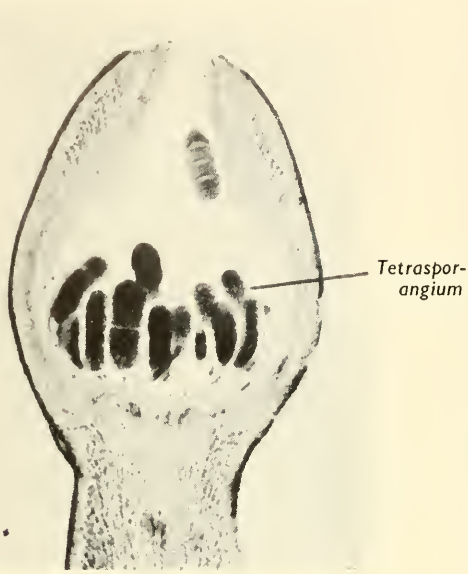

Fig. 174.—*Corallina officinalis.* Longitudinal section of a tetrasporangial conceptacle with tetraspores.

In a diplobiontic life-history, if the two plants are morphologically identical, the alternation between them is said to be **homomorphic.** This applies to *Cladophora*, *Dictyota* and *Polysiphonia* in the above list. In the opposite case, where the plants are dissimilar, the alternation is called **heteromorphic.** This applies to *Coleochaete*, *Laminaria* and *Cutleria* among those mentioned above.

The use of these terms is quite independent of the cytological life-cycle, and it matters not whether the plants concerned are monoploid or diploid. For example, as we have seen above, the life-histories of both *Batrachospermum* and *Fucus* are haplobiontic, but the vegetative phase of the former is monoploid, while that of the latter is diploid. On the other hand in a diplobiontic life-cycle it is inevitable that one vegetative plant of the cycle must be monoploid while the other must be diploid.

It follows therefore that, in considering the type of alternation of generations exhibited by an Alga, the criterion is not whether the plant is monoploid or diploid but whether one or two separate plants are necessary to complete the life-cycle (Fig. 175).

A plant in which the vegetative phase is monoploid is termed a **monoplont** or **haplont,** while one in which the vegetative phase is diploid is termed a **diplont.** Further, if there are two vegetative phases, whether similar or dissimilar, the species is called **haplo-diplont.** These terms refer solely to the cytological condition and are not dependent upon the type of alternation of generations exhibited by the species.

The Rhodophyceae present a further and peculiar condition, brought about by the interpolation of a special post-fertilization carposporophyte tissue which produces the carpospores. This tissue may be quite small or it may be extensive, but it is always produced in organic connection with the gametophyte. In forms like *Batrachospermum* the carposporophyte is the only diploid structure, and thus we have an alternation of two generations, the monoploid gametophyte and the diploid carposporophyte, which are never separated from each other. In such a life-cycle meiosis occurs in the formation of the carpospores. In types like *Polysiphonia*, *Chondrus*, *Ceramium* and *Corallina* the carpospores give rise to independent diploid tetrasporic plants, so that here we have in effect an alternation of three generations, two of which, namely, the gametophyte and tetrasporophyte, are quite independent. In this case the gametophytic plants are monoploid, while both the carposporophytic and tetrasporic plants are diploid. Meiosis, however, does not occur in the carpospores, but is postponed until the formation of the tetraspores.

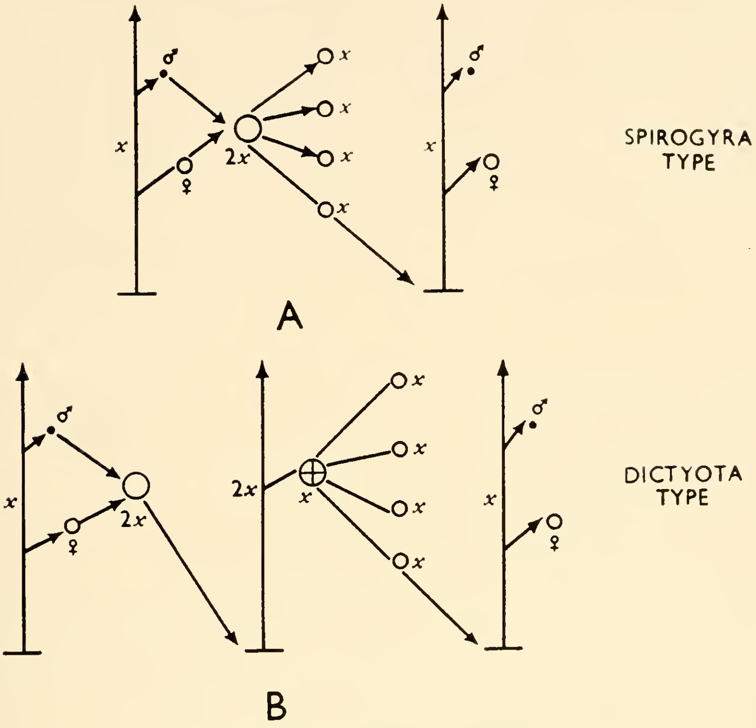

Fig. 175.—Comparison of types of Life-cycle.
A, Haplobiontic. B, Diplobiontic.

The Distribution of Algae

From what has been said already it will be realized that, while the Chlorophyceae occur chiefly in fresh water, the Phaeophyceae and Rhodophyceae are predominantly marine Algae. It has been shown that there appears to be a direct correlation between the conditions of life and the colour of the pigment. Green Algae can only assimilate when growing in bright light, while the Brown Algae can do with rather less, and the Red Algae with least of all.

From the types we have described it is clear that members of the Chlorophyceae occupy a great variety of situations. Quite apart from fresh water, which is their most typical habitat, certain groups live exclusively in the sea, while others, such as *Cladophora*, adapt themselves readily to either salt or brackish water, to life on salt marshes and similar places. Recent investigations have shown that many Algae can be isolated from the soil, and it seems clear that many of the unicellular types live primarily in damp soils.

One of the most interesting aspects of algal distribution, however, is the zonation to be seen on the seashore. If a study be made of the succession of types met with, from high tide mark to well below the lowest levels of the spring tides, it will be found that the genera and species will generally appear in the same order, provided other factors are the same. Exposed on the surface of rocks, only covered by the spring tides, will be found the Channelled Wrack (*Pelvetia canaliculata*) and the Spiral Wrack (*Fucus spiralis*) (Fig. 176).

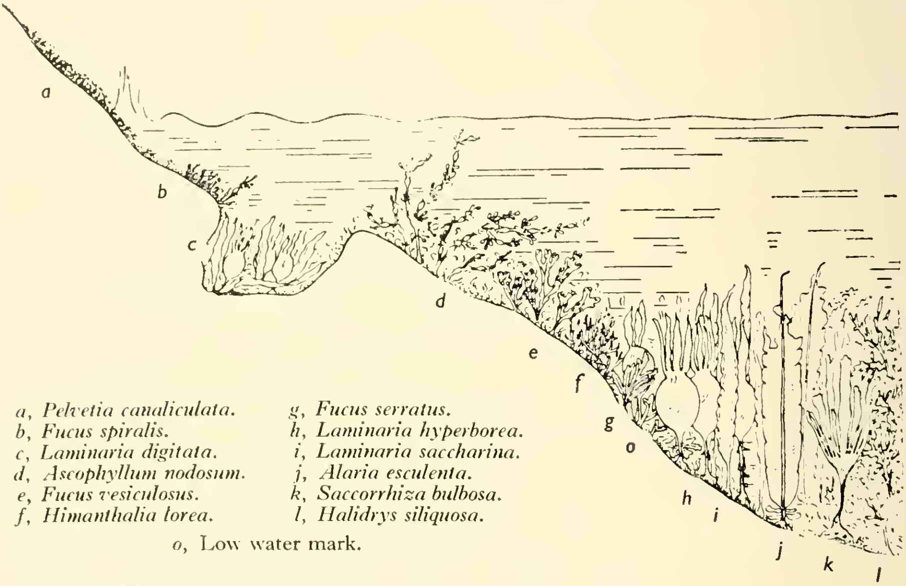

FIG. 176.—Zonation of Algae on sea coast, according to depth below high tide level. (*After Darbishire.*)

Somewhat lower down on these rocks the Knobbed Wrack (*Ascophyllum nodosum*), the Bladderwrack (*Fucus vesiculosus*) and the Serrated Wrack (*Fucus serratus*) form a zone. These Algae are only immersed at high tide and have to withstand considerable exposure to sun and rain.

As we pass further down between tide marks we find that various Red Algae make their appearance, *Laurencia pinnatifida*, *Gigartina stellata* and *Corallina officinalis* being the most common and making another recognizable zone. At about low tide mark species of the Kelps or Tangles (*Laminaria digitata* and *Laminaria saccharina*) appear ; sheltering under their great fronds are many small Brown and Red species. Slightly lower still the Seathongs (*Himanthalia lorea*) appears, with its great thong-like branches sometimes 6 ft. long, and the Badderlocks (*Alaria esculenta*), with a broad frond sometimes as much as 6 ft. in length. Lowest of all the Brown Algae comes the giant *Saccorrhiza bulbosa*, growing in several fathoms of water and producing thalli more than 12 ft. long.

Such plants when growing in large numbers cast a gloom through the water, and among the fronds there is only sufficient light for members of the Rhodophyceae to live. In the forests formed by these Laminarias every rock and cranny is covered by small Red Algae. Only these Algae can live and thrive under such conditions, by virtue of the red pigments which they possess, which are supposed to enable them to absorb the predominating bluish light under water. We need not enumerate here the various species which occur, but we must realize that under these conditions they are much more luxuriant than the stunted specimens we find sheltering under *Fucus* plants on the higher zones of the shore.

It has been observed that certain species of seaweeds show a tendency to move downwards towards lower zones of the shore during the winter months, while others, in contrast, migrate landwards.

Quite apart from the larger Algae, whose distribution we may study on the seashore or the lakeside, there are countless microscopic species, which contribute to that floating population of organisms collectively spoken of as plankton. Many of these species multiply at a surprising rate, sometimes covering the whole surface of a pond in a few days with an almost pure culture of some particular organism, only to disappear again as quickly as they have come.

Many and complex are the problems associated with the distribution of the Algae, but sufficient has been said to indicate the scope of the subject and, it is hoped, to stimulate the reader to further observations of his own.

The Metabolism of Seaweeds

The habitat of a seaweed differs greatly from that of the majority of land plants so that it is only natural to find that they have a number of physiological peculiarities.

When submerged they receive light that has been filtered through varying depths of sea water and which is, in consequence, deprived of most of the red and yellow rays which are those chiefly absorbed by chlorophyll. The view has been widely held that the red and brown pigments are functionally important in that they can absorb the blue and green rays of sunlight and so obtain photosynthetic energy for the plant when under water. Red Algae can grow down to depths of about 12 fathoms on our coasts and much deeper in clear seas, but in dull weather the maximum rate of photosynthesis appears to be at or near the surface and in bright weather about 2 fathoms down. This does not altogether bear out the adaptation idea, and suggests that the red colour is possibly only a protection for the chlorophyll against over-bright sunlight, and that the seaweeds are simply shade plants with particularly sensitive chlorophyll. It is perhaps worth noting here that only chlorophyll a occurs in the Red and Brown Algae, the other form, chlorophyll β, being absent. On the shore the dominant physiological factor is undoubtedly exposure, which includes both bright light and desiccation. The rate of drying is greatest during the first few hours of exposure. Algae growing high up lose water more slowly than those lower down, but the total loss is greater and may reach nearly 70 per cent. of the original weight. No doubt this loss falls principally on the intercellular mucilage and to some extent on the material of the thick cell walls, so that the protoplasm is protected from destruction, but when dry, assimilation is completely inhibited by the slowness of gaseous diffusion through the dry tissues and respiration is extremely slow. Thus growth is much less in the high zones than in the lower zones. Chemical composition also plays a part in protection, for the Algae of the highest zones have the highest fat content, and those of the lowest zones the highest content of carbohydrate, the two being inversely related in the intermediate zones. It has also been found that *Fucus* tolerates much greater changes of temperature than Algae of the lower levels, *e.g.*, *Laminaria*, which appears to be correlated with regular exposure of the former to sunshine at low tide.

In rock pools conditions are quite different. Here there is no desiccation and assimilation can continue at low tide. In small pools with a rich algal flora, however, the Carbon dioxide content of the water is soon exhausted. This leads to dissociation of the bicarbonates of Calcium and Magnesium present in solution. The carbonates of these metals are only slightly soluble, but they suffice to give the water a strongly alkaline reaction, which increases steadily with the length of the inter-tidal period. In the highest pools only a few seaweeds can withstand the effects of this high alkalinity, and such pools have a very limited flora, mostly of Chlorophyceae.

Perennation of Seaweeds

As no resting stage is known in the life-history of any seaweed, it was for long a problem how they passed through the winter season. Many seaweeds are invisible at this time, while others disappear during periods at other times of the year. The solution was discovered by Sauvageau, who found that at these times the plants are represented by very small, almost microscopic thalli, which are prostrate and discoid or filamentous in structure. Numerous Algae have been found to show this alternation, among them being *Ectocarpus* and *Cutleria*.

These microthalli are called the **adelophycean stage.** They seem usually, perhaps always, to be monoploid and to reproduce the macroscopic plant sexually, by gametes formed in gametangia. If this is the case they form an interesting comparison with the microscopic gametophytes of *Laminaria*.

The separation of prostrate and upright generations among these Algae may be regarded as a further development of the **heterotrichous habit** shown by many Algae in all groups, namely the distinction between prostrate and upright portions of the thallus. Fritsch has laid great stress upon the widespread occurrence of this habit among the Algae as foreshadowing and perhaps actually originating the distinction between prostrate or reduced gametophytes and upright sporophytes which is characteristic of the lower land plants.

CHAPTER VI

THE FUNGI : ARCHIMYCETES AND PHYCOMYCETES

The Fungi are generally included as the second group of the phylum Thallophyta. Some authorities, as we have already indicated, regard the Fungi as a group of organisms of independent origin which cannot be correctly included in a natural classification of plants, since, they argue, Fungi are not plants at all. To follow such an argument to its limit it would be necessary to postulate not two but three kingdoms, Plants, Animals and Fungi. It is outside the scope of this book to discuss the relative merits of these two views, and though there is much to be said in favour of the latter we shall, for the sake of simplicity of treatment, regard the Fungi as members of the Thallophyta.

Whatever may be their correct systematic position the Fungi are a very large and important group. There are something like 37,500 species definitely known, and probably about three times that number in existence. About 9,000 species are known from Britain. Two of the largest orders are the Urediniales and the Agaricales which include more than 4,000 species apiece.

Fungi may be readily separated from green plants by the absence of chlorophyll, and, since they do not feed holozoically, they must of necessity live either as **parasites** on other organisms or as **saprophytes** on organic compounds. The mode of nutrition exhibited by the Fungi varies to some extent, but, in general, they make use of carbohydrates, amino-acids and other organic substances. They also absorb nitrates, ammonia, phosphates and sulphates. Such metals as Sodium, Calcium and Magnesium do not appear necessary for their metabolism, though they may be essential to higher plants. Some Fungi, however, appear to require traces of some of the heavy metals such as Zinc, which are not generally necessary.

With few exceptions all Fungi can live as saprophytes on nutrient media composed of soluble organic substances, and it is in this way that many hundreds of cultures are kept in laboratories for study. In fact many Fungi which in nature appear to live exclusively as parasites are able to grow saprophytically under cultural conditions. This plasticity of Fungi is one of their most important features, coupled with a faculty for changing their appearance to a considerable extent according to the composition of their food. Many Fungi exhibit **pleomorphism,** that is, the power of assuming various shapes not only in culture but also under natural conditions, a fact which has greatly complicated their systematic study.

In all but the simplest groups the vegetative thallus consists of a web of filaments termed **hyphae** which together make up the body or **mycelium.** This mycelium may either develop on or in the substrate, in the case of saprophytes, or inside or on the surface of the host in the case of parasites.

The hyphae may be either coenocytic or may consist of cells, each possessing one or sometimes two nuclei. In the higher groups the wall of the hyphae is composed of **fungus cellulose,** which differs from ordinary cellulose in the fact that it does not stain violet with Iodine and sulphuric acid. True cellulose walls occur in certain of the lower groups.

The reproductive bodies in the lower groups may be small and inconspicuous, but among the higher members it is the fruiting bodies which are the only obvious part of the fungus, as, for example, in the Mushroom, where the mycelium is underground and passes unnoticed. In almost all groups asexual reproduction by spores occurs, and in many it represents the more general and prolific method of propagation, though in any case the ultimate result of sexual reproduction is also the formation of an abundant crop of spores. In the higher groups the sex organs become more and more reduced until often all that remains as an expression of sex is the union of two nuclei which may be of vegetative origin.

The Fungi are classified according to the way in which the spores are produced :—

1. **Archimycetes** (*e.g.*, Club Root Fungus).
2. **Phycomycetes** (*e.g.*, Pin Moulds and Water Moulds).
3. **Ascomycetes** (*e.g.*, Morels, Truffles and Blue Moulds).
4. **Basidiomycetes** (*e.g.*, Mushrooms, Toadstools and Puff Balls).
5. **Fungi Imperfecti** (see under " Plant Pathology " in Volume IV).

In the Archimycetes and Phycomycetes the spores, and frequently the zoospores, are borne in large numbers in **sporangia.** In the Ascomycetes the spores are produced in an **ascus** or sac, each ascus containing usually eight **ascospores.** In the Basidiomycetes the **basidiospores** are produced externally in fours on a club-shaped **basidium.** The Fungi Imperfecti produce only asexual spores.

ARCHIMYCETES

The Archimycetes are Fungi devoid of a mycelium, the body of the organism consisting of a naked mass of cytoplasm termed a **plasmodium,** which finally, after a period of vegetative growth, becomes converted into one or more **sporangia.** These sporangia may be simple or elaborate structures containing a large number of spores. The spores on germination give rise to motile **swarm cells** which function as gametes, fuse in pairs and produce a fresh vegetative plasmodium.

The organisms may be saprophytic or parasitic and are quite common. They probably represent primitive groups of organisms which have not contributed anything to the evolution of the main groups of the Fungi but are rather side lines which have not proved specially successful, but which still exist to the present day as survivals of an early type of fungal organization.

The limits of this group have been variously held by different authors to include a greater or smaller number of orders of the lower Fungi. Possibly the simplest, though not necessarily the most correct view, is to consider the Archimycetes as embracing three orders, all of which must be regarded as side lines in evolution, while placing the only order which appears to have contributed to the higher Fungi, namely the Chytridiales, in the Phycomycetes.

According to this scheme we are left with three orders :—

1. **Myxomycetales,** sometimes called the Mycetozoa, which are saprophytes.
2. **Acrasiales,** in which the plasmodia readily fragment into separate amoeboid cells and which live as saprophytes on dung.
3. **Plasmodiophorales,** which are parasites of higher plants.

We shall refer briefly to the general characters of the Myxomycetales and consider one type of the Plasmodiophorales.

Myxomycetales

With the exception of one genus, *Ceratiomyxa*, to which we shall refer later, all the members of this order live on the surface of dead wood, leaves and the like.

The diploid organism formed as a result of the fusion of swarm cells is termed a **myxamoeba** and resembles a true Amoeba. It can migrate by means of **pseudopodia,** that is, by extending a part of its protoplast followed by a flowing movement of the whole body in the direction of the pseudopodium thus formed. In this way it can move at a not inconsiderable pace. The myxamoeba is devoid of any cell wall, and the protoplast only possesses a rather thicker and tougher **ectoplasm** through which food material in solution is absorbed. The protoplast can, however, engulf, by flowing around them, small objects such as bacterial cells, which it appears able to digest. In this way the body grows and increases in size, becoming a multinucleate structure termed the **plasmodium** (Fig. 177). Several myxamoebae may contribute to the formation of a plasmodium and any unconjugated swarm cells may also be incorporated into the plasmodium, which may thus, in time, both by feeding and accretion, become a body of considerable size ; in fact, plasmodia containing as much as a litre of living protoplasm have been found quite frequently. During this period the plasmodium may become coloured, and, though white plasmodia are common, sulphur yellow or pink are characteristic of some species. The plasmodium now contains a very large number of nuclei produced by the division of pre-existing ones.

When the plasmodium is mature, **sporangium** formation begins (Fig. 178). This may result in the conversion of the whole plasmodium into a single giant sporangium termed an **aethalium,** or a number of separate sporangia may be formed. In the latter case the sporangia may be sessile but are more usually stalked (Fig. 179).

During the differentiation of the sporangium an elaborate system of internal threads is laid down as a result of the filling up of cleavage furrows in the protoplasm of the young sporangium with chitinous material. This system of threads is called the **capillitium** (Fig. 180), and it is sometimes attached to a prolongation of the stalk. The sporangium also secretes a hard brittle wall. Granules of calcium carbonate frequently cover the surface of the wall, and are also formed in the meshes of the capillitium. During the formation of the spores a meiosis occurs, so that the mature spores are monoploid.

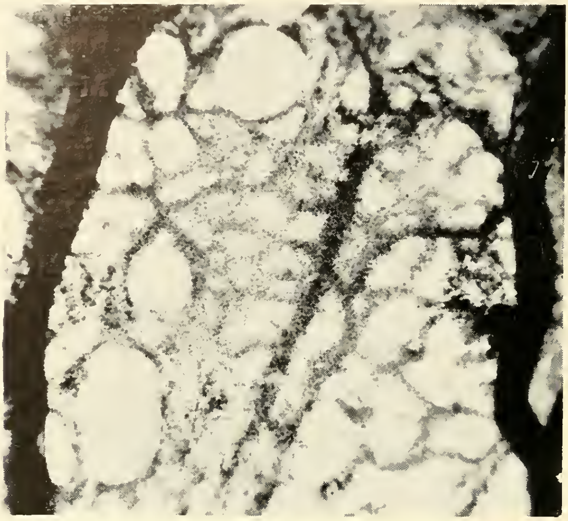

FIG. 177.—*Badhamia sp.* Portion of plasmodium showing thickened strands and finer reticulations. Stained to show the very numerous small nuclei.

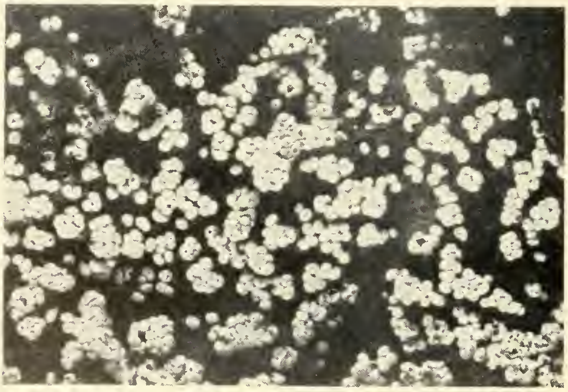

FIG. 178.—*Badhamia punicea.* Sporangia. Natural size.

The **spores** are liberated by the bursting of the wall of the sporangium. This also exposes the capillitium, which is hygroscopic and twists about as it absorbs or loses water, thus breaking up the spore mass. The spores are minute, round bodies, often with beautifully sculptured walls.

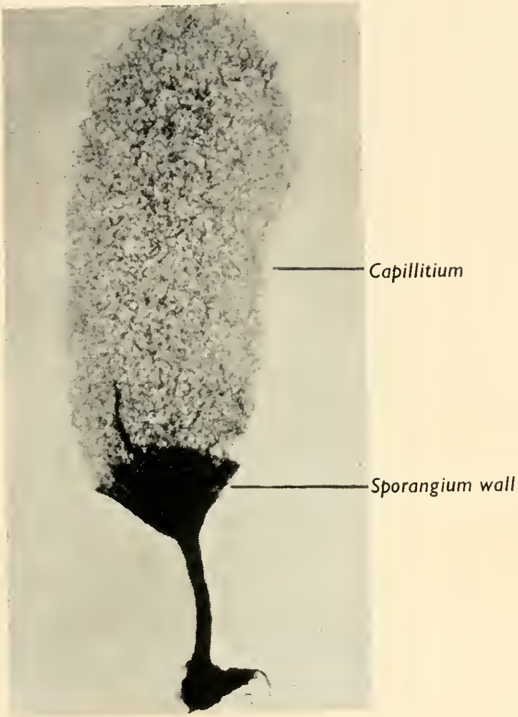

FIG. 179.—*Arcyria denudata.* Sporangium after dehiscence showing capillitium.

FIG. 180.—*Arcyria denudata.* Portion of the capillitium highly magnified.

On germination the spore gives rise to a single spindle-shaped **swarm cell,** which is provided with two apical flagella, one of which is longer than the other (Fig. 181). The time taken for the spores to germinate varies with the species, but laboratory tests by growing them in a sugar solution show that while some species, *e.g.*, *Reticularia lycoperdon*, may germinate in a few hours, others take two to three weeks to produce swarm cells. After liberation from the spores the swarm cells fuse in pairs at once and give rise to binucleate zygotes or **myxamoebae,** from which a new plasmodium will arise (Fig. 182) in which the nuclei fuse in pairs, a process called **karyogamy.**

FIG. 181.—*Reticularia lycoperdon.* Germination of spores to release swarm cells.

In the genus *Ceratiomyxa* mentioned above (Fig. 183) the development is somewhat different, for the plasmodium lives internally within dead or decaying wood and only produces fine processes termed **sporangiophores** externally. These bear minute sporangia which are oval in shape and pure white in colour. It is said that each sporangium, which is frequently referred to as a spore, gives rise to about eight swarm cells. The individual spores in other genera produce only one.

Species of the Myxomycetales are very common among dead wood and leaves in damp woods and are extremely beautiful objects. Though the individual sporangia are often no larger than a pin's head they are generally produced together in sufficient numbers to be seen easily. A careful search of any damp wood or damp pile of sticks or straw will be certain to yield a number of different species.

Plasmodiophorales

The Plasmodiophorales are parasitic Archimycetes in which the plasmodium lives in the cell of a higher plant. By means of fragmentation the plasmodium may break up, and by passing from one cell to another during cell division of the host plant it may become widely distributed in the host tissues. The group is a small one represented by less than two dozen species. They are mostly very rare, but two species, *Plasmodiophora brassicae*, which causes Club Root or Finger-and-Toe disease of Cruciferae, and *Spongospora* *subterranea*, which is responsible for Powdery Scab of Potatoes, are of considerable economic importance.

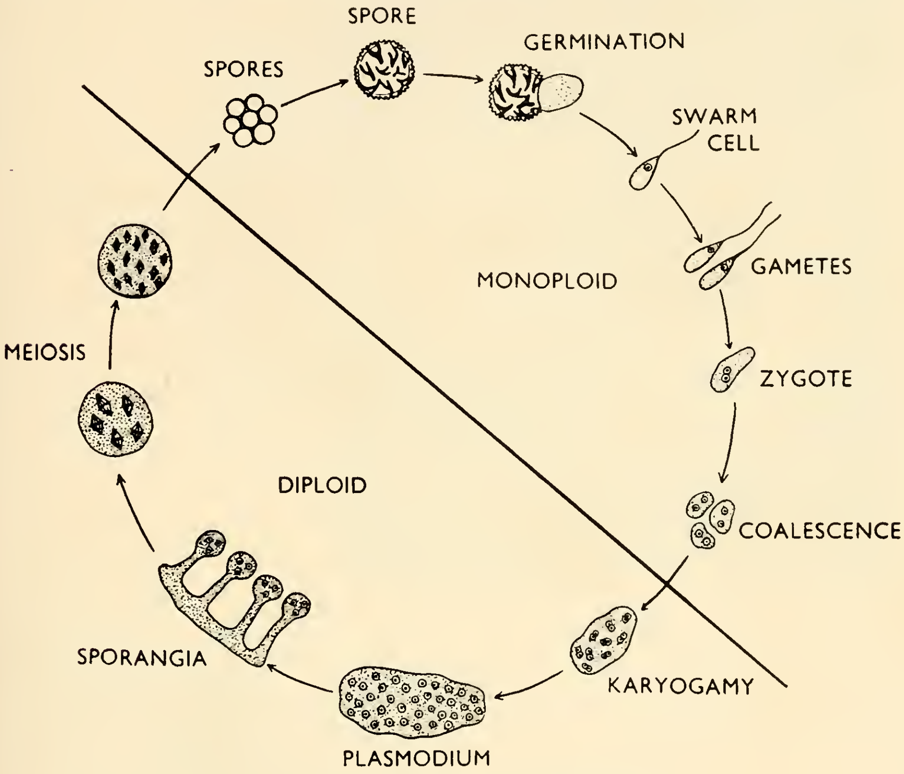

Fig. 182.—Life-cycle of a *Myxomycete*.

We shall take *Plasmodiophora brassicae* as a type of this order.

Plasmodiophora brassicae (Finger-and-Toe Disease or Club Root of Cabbages)

Club Root Disease is the name given to a characteristic swollen malformation of the roots of cruciferous plants (Fig. 184). It is particularly common on acid soils and frequently causes great loss to market gardeners. The Fungus gains entry to the young root tissues through the root hairs and stimulates great hypertrophy of the tissues.

In a transverse section through an infected root it will be seen that the normal arrangement of the tissues has been altered by the formation of many additional cells, splitting up the original vascular system and

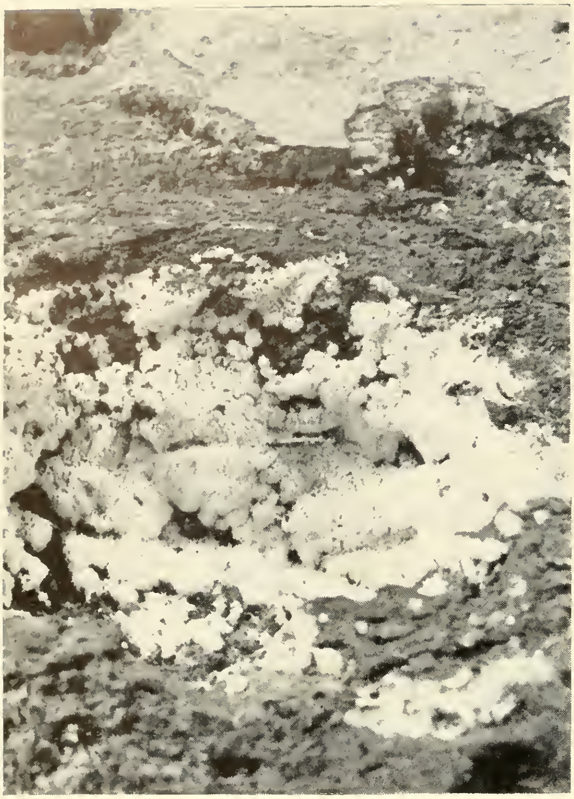

FIG. 183.
Ceratiomyxa fruticulosa growing on log. Natural size.

FIG. 184.
Plasmodiophora brassicae. Club root disease on Cabbage showing hypertrophy of diseased roots.

producing wide bands of thin-walled tissue (Fig. 185). This is manifested externally by the swelling or **hypertrophy** of the root, which is the reason for the popular name given to the disease. In these thin-walled cells lie the **myxamoebae,** which are at first uninucleate. They increase in size, absorbing the food material in the host cells, and they may divide, so that if division of the host cell occurs both the daughter cells become infected. When the tissue becomes more permanent the myxamoeba settles down and grows, without dividing, into a multinucleate **plasmodium** (Fig. 186). When it

FIG. 185.—*Plasmodiophora brassicae.* Transverse section of hypertrophied root showing enlarged medullary rays and spore masses in cells of the ground tissue.

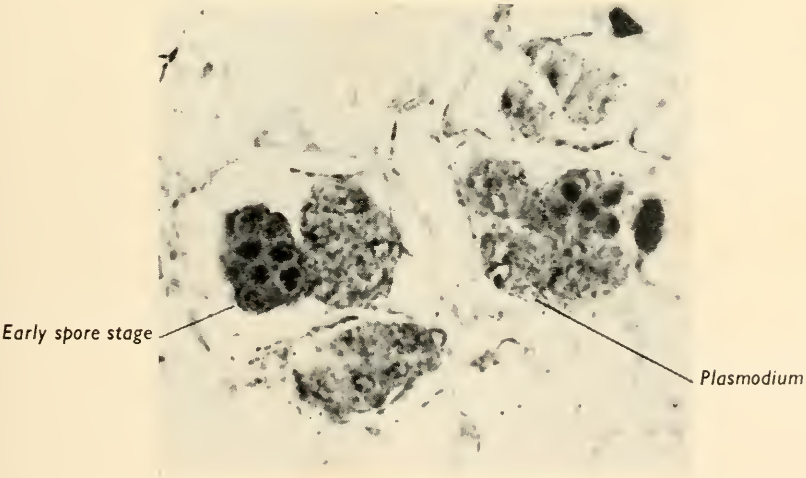

FIG. 186.—*Plasmodiophora brassicae.* Multinucleate plasmodia in tissue cells of host root.

has exhausted the food supply, meiosis occurs and the whole plasmodium becomes separated into uninucleate portions, around each of which a wall is laid down. Thus the host cell becomes filled with a mass of **spores** (Fig. 187).

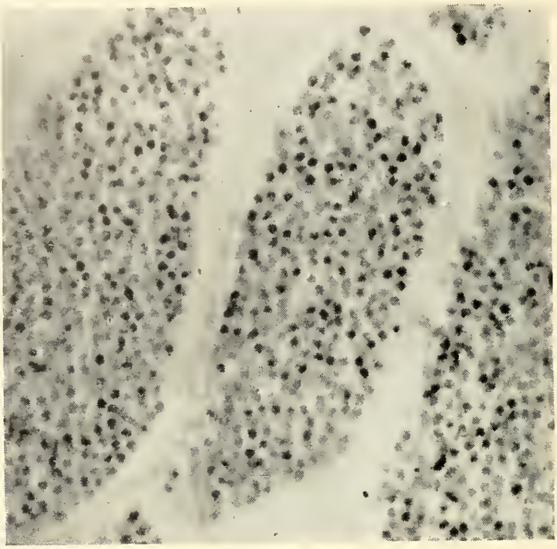

Fig. 187.—*Plasmodiophora brassicae.* Host cells filled with spores.

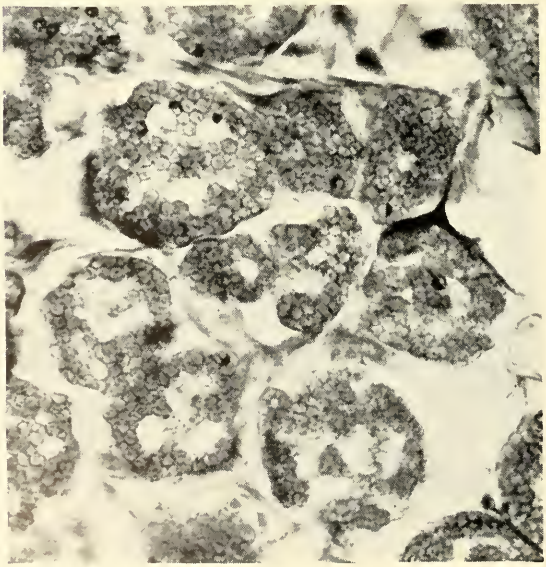

Fig. 188.—*Spongospora subterranea.* Spores in cells of infected Potato. Note the different arrangement of the spores in this genus and in *Plasmodiophora.*

In other genera the spores derived from a plasmodium do not separate, but form a group with a more or less regular and characteristic shape, and it is chiefly by this means that the genera are distinguished from one another. In *Spongospora subterranea* the spore mass forms a ball of irregular shape which has hollows in it and can be compared to a sponge, whence the name *Spongospora* was derived (Fig. 188).

The spores are liberated by the breakdown of the host tissue and are thus set free into the soil. Here they germinate to produce **zoospores,** which are pyriform in shape and possess each two flagella, one directed forwards and another, very much shorter, which may be directed sideways or backwards. These zoospores have the power of penetrating the root hairs, and once inside give rise to **gametangia** (Fig. 189), which are very small spherical bodies, the contents of which divide into a small number of motile **isogametes.** These fuse in pairs to form fresh myxamoebae. Whether the migration from the root hairs to the root takes place before or after fusion of the gametes is not known, but the myxamoebae are found mainly in the meristematic cells of the young root, where they stimulate active cell division and in this way are themselves widely distributed in the host tissue.

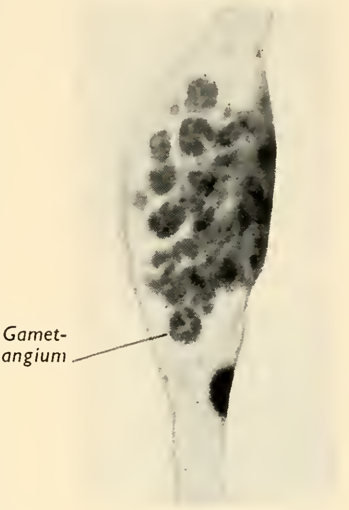

FIG. 189.—*Plasmodiophora brassicae.* Gametangia in root hair of host plant.

In *Spongospora subterranea* it is the cortical tissue of the tubers which is most characteristically attacked and the hypertrophy is restricted to the formation of scabs, the surface of which becomes powdery as the spore-masses mature. When the roots are attacked, however, hypertrophy may sometimes be very marked, and the effect of the disease resembles superficially the Wart Disease, *Synchytrium endobioticum* (see p. 203). (Fig. 190.)

The cytology of *Plasmodiophora* (Fig. 191) and indeed all the members of the order is peculiar and unique. During the development of the plasmodium all the nuclei within it divide simultaneously by a process termed **protomitosis,** which differs from a normal mitosis in certain features. The metabolic nucleus does not possess a typical reticulum but instead the chromatin is disposed in a peripheral zone, leaving a clear, central, nuclear vacuole in which lies a single spherical **karyosome.** During the prophase of the division the peripheral chromatin becomes denser and the nuclear membrane becomes drawn out into an ellipsoidal shape. At metaphase the chromatin forms a median ring surrounding and enclosing the karyosome, which now becomes drawn out and finally dumb-bell shaped, the nuclear membrane persisting throughout the division. The chromatin ring now splits into two rings which move away from one another, keeping pace with the dividing karyosome. Whether this ring is a single unit or whether it is made up of four separate chromosomes has not been finally decided. In the anaphase of the division the two rings become completely separated and the karyosome divides into two, so that in the telophase of the division the chromatin ring of each daughter nucleus again encloses a single karyosome. The nuclear membrane now constricts and separates into two to form the membrane around the daughter nuclei.

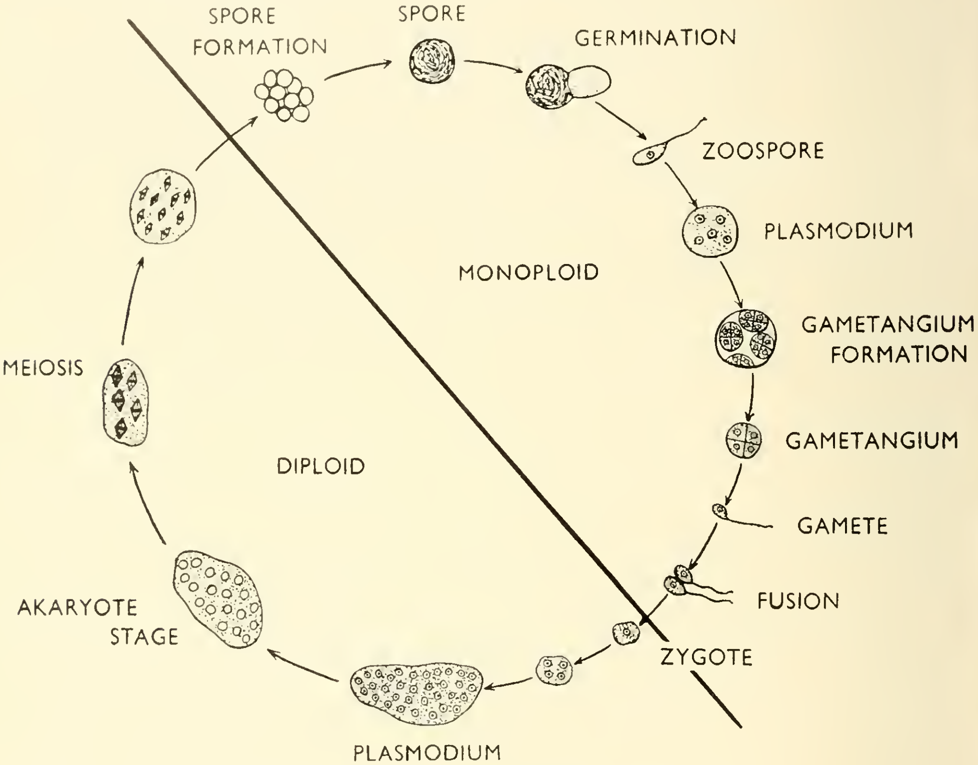

Fig. 190.—Life-cycle of *Plasmodiophora brassicae*.

Prior to the formation of spores a further change is observable in the behaviour of the nuclei, which is referred to as the **akaryote** stage. During this stage chromatin is apparently discharged from the nuclei into the cytoplasm, so that both the peripheral chromatin and the karyosome disappear and the nuclei can be recognized only as clear areas in the cytoplasm of the plasmodium. Chromatic discharge at some stage in the life-cycle has been described in other members of the lower Fungi, especially in *Synchytrium*. The reappearance of chromatin within the nuclei coincides with the prophase of the heterotypic division of meiosis. In these two divisions prior to the formation of spores a typical nuclear spindle appears, and separate chromosomes are apparently formed. No nuclear membrane is present, and it is doubtful if it is reformed between the beginning of the

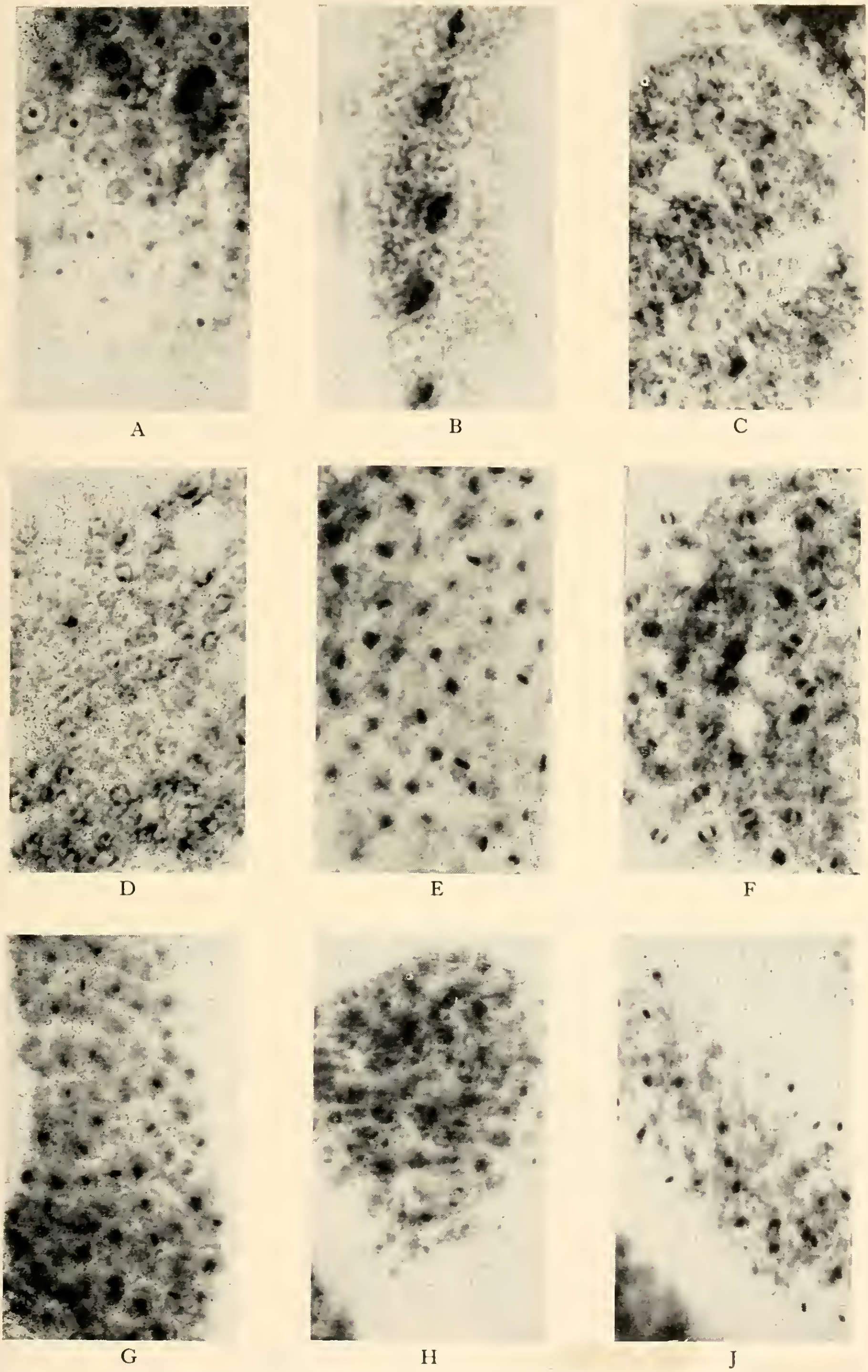

FIG. 191.—*Plasmodiophora brassicae.* Cytological phases of the life-cycle. A, Resting nuclei in plasmodium, with peripheral chromatin and karyosome. B, Metaphase of protomitosis. C, Early akaryote stage with no karyosome and chromatin diminishing. D, Late akaryote stage. E, Heterotypic metaphase. F, Heterotypic anaphase. G, Homotypic metaphase. H, Homotypic anaphase. J, Homotypic telophase.

akaryote stage and the production of metabolic monoploid nuclei in the spores themselves.

A nuclear division similar to that in the Plasmodiophorales has been described in certain of the Protozoa, which has led to the suggestion of a common ancestry of the two groups. In the Myxomycetales, on the other hand, the nuclear divisions in the plasmodium are mitotic.

PHYCOMYCETES

The Phycomycetes are Fungi in which the thallus is composed of single cells or of filaments of cells forming hyphae. Frequently these hyphae are coenocytic, transverse septa occurring either rarely, in the older hyphae, or exclusively at the separation of the reproductive organs. The hyphae may be multinucleate and the nuclei are frequently extremely small.

Sexual reproduction is either by motile isogametes, in the lowest order, or by means of an oogonium and antheridium. The oogonium may produce from one to many oospheres. The antheridium rarely produces free antherozoids, and fertilization is normally effected by direct contact through a fertilization tube. The oospore is usually thick walled and functions as a resting spore. It may germinate directly to form hyphae or by the development of zoospores. In the Mucorales peculiar conditions obtain, sexual reproduction being by isogametes or anisogametes which are invariably non-motile.

Asexual reproduction in the lower groups is by zoospores, which may have either one or two flagella, a character to which some workers attach considerable importance and use as a basis of classification. In the higher members either sporangia are produced containing spores which germinate directly into a hypha or aerially distributed conidiospores may be abstricted in chains from the apices of special hyphae termed conidiophores.

The species are predominantly aquatic and may live either as parasites or saprophytes. Some occur in soil and others as endoparasites of higher plants, and it is in these latter forms that we see the transition from an aquatic to an aerial method of spore distribution being evolved. By virtue of their aquatic habit and their marked similarity to certain Algae they were at one time regarded as Algae which had lost their chlorophyll and were classified after their supposedly corresponding algal groups. The name Phycomycetes or " Algal Fungi " emphasizes this idea. This view now receives but little support from mycologists.

We shall consider examples from the following orders :—

1. **Chytridiales** (*e.g.*, *Rhizophidium*, *Synchytrium*).
2. **Saprolegniales** (*e.g.*, *Saprolegnia*).
3. **Monoblepharidales** (*e.g.*, *Monoblepharis*).
4. **Peronosporales** (*e.g.*, *Pythium*, *Cystopus*, *Peronospora*).
5. **Mucorales** (*e.g.*, *Mucor*).

Chytridiales

The Chytridiales are Phycomycetes in which sexual reproduction is effected by the fusion of isogametes and no trace of oogamy occurs. The vegetative thallus may be either a plasmodium devoid of a cell wall or it may be unicellular, while in the highest groups it consists of a multicellular or a coenocytic hypha.

The group contains the most primitive members of the Phycomycetes. A few live as parasites in the tissues of higher plants, but the majority are ectoparasites or saprophytes on Algae. In some the life-history is complicated by special adaptation to the parasitic habit and to overwintering in the host, but in many the life-history is remarkably simple and demonstrates the way in which the group may have evolved. In general, it may be said to consist of two stages, the first an amoeboid vegetative phase, followed by a flagellate reproductive stage. As we pass up the group to the more complex types the tendency appears to have been to reduce the amoeboid or plasmoidal stage and to enclose the protoplast in a wall, which then becomes the wall of a sporangium in which eventually the reproductive organs arise.

We shall consider two types, the one *Rhizophidium globosum*, representing the ectoparasitic type, and the other *Synchytrium endobioticum*, the endoparasitic mode of nutrition.

Rhizophidium globosum

This little organism is by no means well known, though actually it is very common. It occurs with other closely allied species on the filaments of Green Algae, particularly *Spirogyra* and *Cladophora*, and may be found at almost any time of the year in ponds or streams.

The mature plant consists of a spherical sac attached to the surface of the algal filament by a short **rhizoid** (Fig. 192). The extent of development of this rhizoidal system is a specific character; in some species it is little more than a peg which does not penetrate the cell wall of the host, in other species the wall is penetrated and a system of rhizoids develops inside which may ramify over the chloroplast of the host cell, suggesting that food material is withdrawn through the rhizoids.

Fig. 192.—*Rhizophidium globosum*. Zoosporangium on wall of *Spirogyra* filament. Note disorganization of host chloroplast.

REPRODUCTION

The whole body of the Fungus functions as a **zoosporangium** and its contents divide up into a large number of uniflagellate, spherical **zoospores** which escape through an operculum formed at the top of the sporangium (Fig. 193). Whether these bodies ever fuse in pairs or not is unknown, though this has been recorded in allied genera. The motile cell soon settles down by its flagellated end, and the flagella are withdrawn. From the attached end the rhizoidal system is developed, while the remainder of the cell enlarges and grows into a sac resembling the parent, which will in time become a fresh zoosporangium.

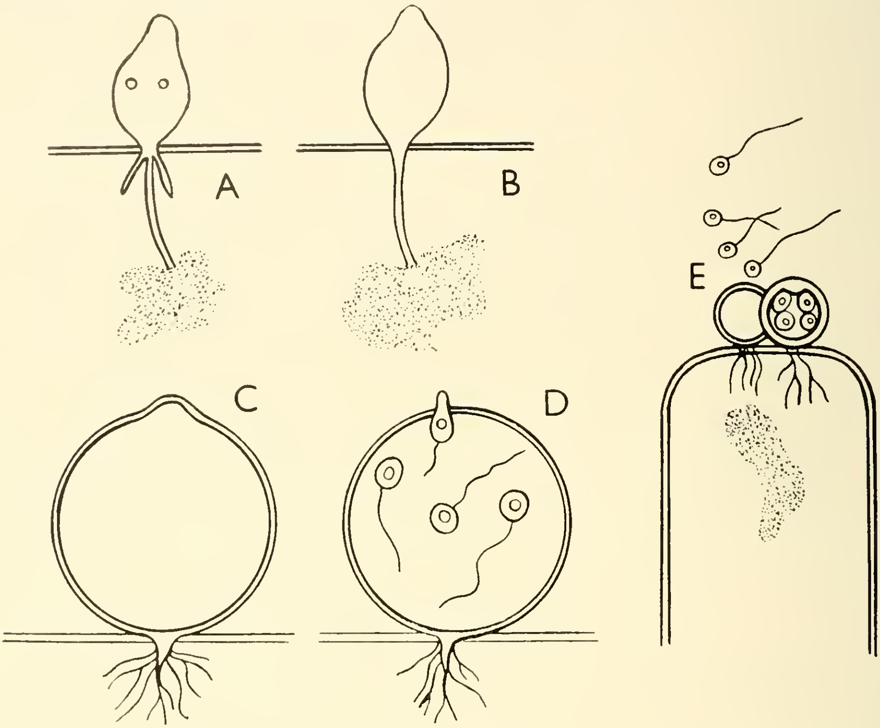

FIG. 193.—*Rhizophidium globosum.* A and B, Zoospore penetrating wall of host cell, with development of rhizoids. C, Mature zoosporangium. Contents not shown. D, Escaping zoospores. E, Small zoosporangia on host cell. (*After Atkinson.*)

An interesting development which is worth referring to here is seen in certain allied genera. In some, after the development of the rhizoidal system, a swelling appears immediately inside the host wall which is termed the **subsporangial swelling.** In certain genera this remains small and it is the cell outside which forms the zoosporangium. A series of examples (Fig. 194), however, are known which lead up to a condition where the subsporangial swelling becomes the zoosporangium, while the original external cell remains quite small and after penetration may disappear. At the same time rhizoids develop not merely from the base but all over the surface of the new sporangium. Thus we see one way in which an ectoparasitic fungus may become an endoparasitic one.

The life-cycle of *Rhizophidium* is so simple that it will not be necessary to express it in the form of a diagram.

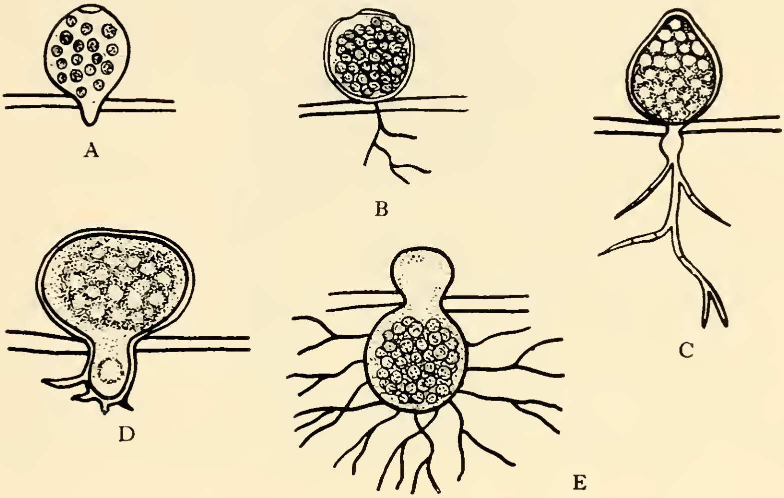

Fig. 194.—Evolution of the subsporangial vesicle. A, *Phlyctidium brevipes.* B, *Rhizophidium cyclotellae.* C, *Chytridium schenckii.* D, *Phlyctochytrium vernale.* E, *Entophylyctis bulligera.* (*After Atkinson.*)

Synchytrium endobioticum (Wart Disease)

This Fungus is a very important plant pathogen, causing the well-known Wart Disease of potatoes, which may cause very great loss of the tubers either in the ground or later in storage (Fig. 195). The disease is common in most parts of the world where potatoes are grown commercially. In comparatively recent years a number of varieties have been produced which are immune to the disease, and such varieties should alone be planted in infected soils. So far as the British Isles are concerned the West of England is more liable to attacks of Wart Disease than either Scotland or the Eastern Counties.

The Fungus responsible for this disease has a relatively simple life-history, though it is considerably more complex than that of *Rhizophidium*, in fact *Synchytrium endobioticum* may be regarded as a member of a specialized side-line from an evolutionary view-point.

In describing the life-history it is desirable to start with the **zoospore,** which enters a cell of the young potato tuber at or about soil level. Once inside, this naked body passes to the base of the host cell and there forms a wall around itself. It rounds off and enlarges greatly, and finally forms a thick, two-layered wall, and is called the **prosorus** (Fig. 196). The nucleus also increases very greatly in size and gives off stainable chromatin material into the cytoplasm. A pore now appears in the outer layer of the wall, and the contents migrate into a sac formed by the extrusion of the inner wall layer. During the migration of the protoplast the nucleus begins to divide until some thirty-two nuclei have been formed, when planes of cleavage appear and walls are laid down, cutting the body into some four or five **zoosporangia,** each enclosed in a separate wall, and the whole lying inside the original inner membrane.

Fig. 195.—*Synchytrium endobioticum.* Wart Disease on Potato.

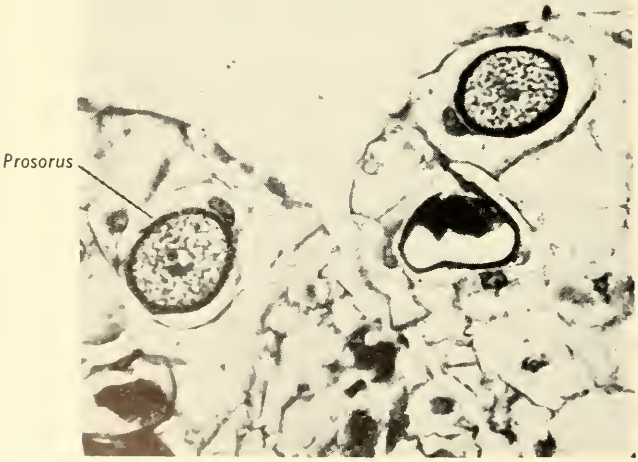

Fig. 196.—*Synchytrium endobioticum.* Section of Potato showing prosori.

In these zoosporangia further nuclear division goes on until about three hundred nuclei have been produced in each sporangium. Around these nuclei zoospores are differentiated. Thus from the original zoospore which entered the host cell some 1,500 zoospores are developed.

The mature **sorus,** which is the name given to the group of sporangia, now absorbs water and swells, rupturing the wall of the host cell and forcing out the separate sporangia, which thus come to lie near the surface of the potato. Through slits, or sometimes through definite projections of the wall, termed **papillae,** the zoospores escape.

REPRODUCTION

The behaviour of these zoospores depends upon the environmental conditions (Fig. 197). If they are liberated from the sporangium immediately

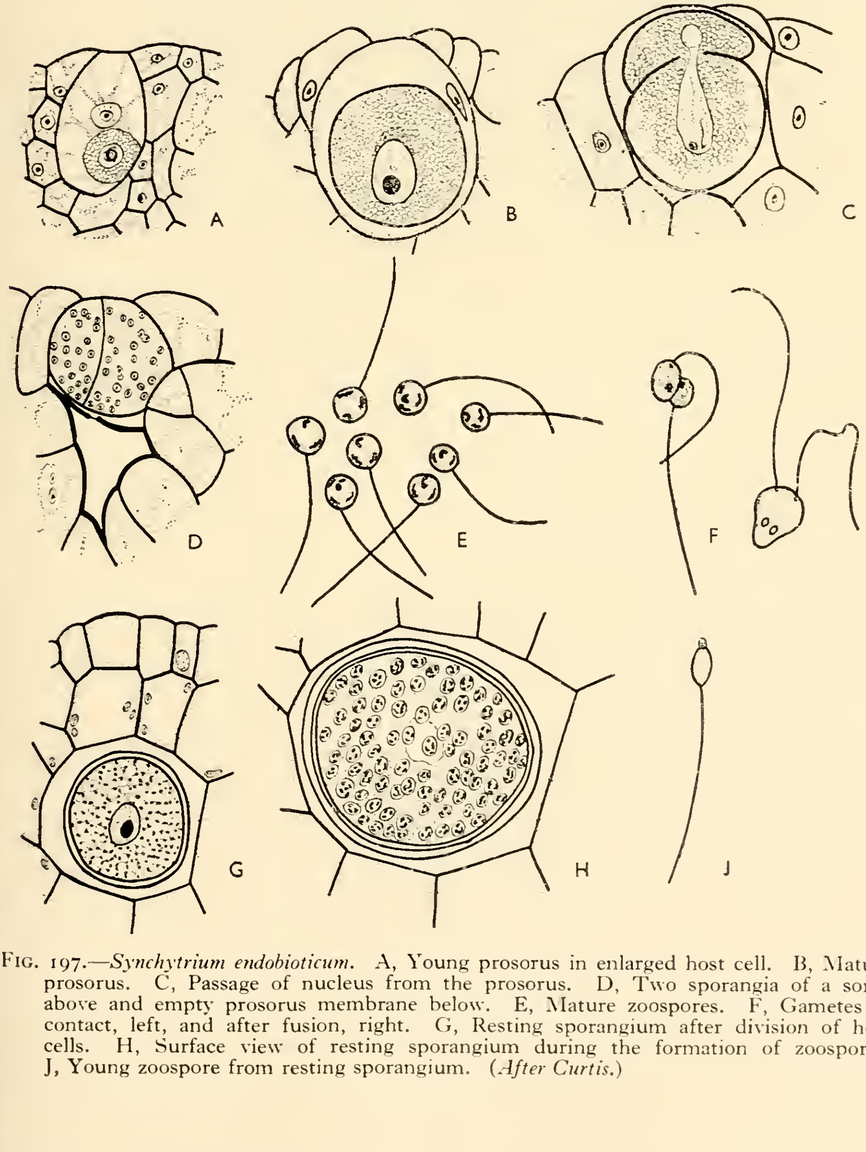

FIG. 197.—*Synchytrium endobioticum.* A, Young prosorus in enlarged host cell. B, Mature prosorus. C, Passage of nucleus from the prosorus. D, Two sporangia of a sorus above and empty prosorus membrane below. E, Mature zoospores. F, Gametes in contact, left, and after fusion, right. G, Resting sporangium after division of host cells. H, Surface view of resting sporangium during the formation of zoospores. J, Young zoospore from resting sporangium. (*After Curtis.*)

they are formed, they function as asexual zoospores and give rise to fresh sori in the way already described. These zoospores are spherical bodies with a very long apical flagellum. When they reach the host cell the flagellum shortens and contracts until finally it is absorbed and the body enters the host tissue as a naked mass. On the other hand, if as a result of lack of sufficient moisture the zoospores are retained within the sporangium for a longer time, they appear to get smaller in size, and on liberation they then function as gametes, fusing in pairs to produce biflagellate zygotes. The zygote also enters the

Fig. 198.—*Synchytrium taraxaci.* Sorus in leaf of dandelion.

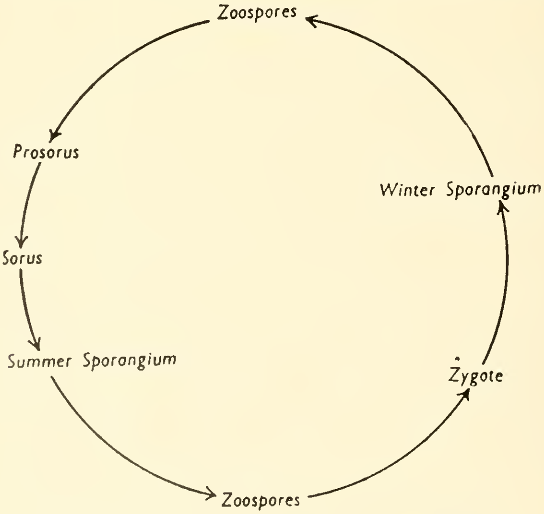

Fig. 199.—Life-cycle of *Synchytrium endobioticum.*

host tissue after the retraction of the flagella and sinks to the bottom of the host cell.

This body then enlarges in size, forming a **resting sporangium** (Fig. 198), which is characterized by having a thick wall composed of three layers. The inner two are derived from the tissues of the parasite, but the third is obtained from material originating from the disorganization of the host cell. The contents of the resting sporangium divide up into zoospores, which are finally liberated by the swelling of the outer layer and the cracking of the inner layers of the wall. These zoospores are oval in shape with a basal nucleus and a single long apical flagellum. It is during the formation of these zoospores that meiosis occurs. They germinate to produce sori in the tissues of the host plant.

In order to distinguish more clearly between the sporangia produced in the sori and those with thick walls produced from the zygotes, the former are sometimes referred to as **summer sporangia** and the others as the **winter sporangia** (Fig. 199).

WART FORMATION

The formation of wart-galls in the host tissue is brought about in the following way. A cell invaded by a zoospore enlarges as the parasite grows, and at the same time the adjacent cells elongate and divide, thus forming a raised rosette of cells around the infected one. Later the cells of the rosette may be secondarily infected by zoospores originating from the sporangia formed in the cell of primary infection. These cells then undergo changes of a similar kind, so that in a short while a mass of gall tissue develops. Cells invaded by the zygotes appear to behave differently. They are stimulated to tangential cell division, and since the zygote lies at the base of the cell the thick-walled sporangium, when formed, is buried in the wart produced.

Saprolegniales

The Saprolegniales are Phycomycetes in which the vegetative mycelium is profusely branched and coenocytic, septa occurring rarely, in older branches and at the separation of the reproductive organs. Asexual reproduction is by zoospores, which exhibit a peculiar condition of development. In the simpler genera the zoospores when liberated are pyriform and have two equal apical flagella. They then rest and encyst, emerging again with equal lateral flagella and reniform in shape. In the more advanced members the earlier phase of this condition, which is termed **diplanetism,** may be missing. Sexual reproduction is oogamous, there being more than one oosphere in each oogonium. The antheridium is a filiform structure and fertilization is by a fertilization tube.

The species may be monoecious or dioecious; almost all are saprophytes and are characteristic inhabitants of soils. Many are also found in fresh water.

We shall consider in detail one example, *Saprolegnia.*

Saprolegnia

The separation of the species and even the genera of the family Saprolegniaceae is by no means easy. The genera are separated mainly by the method of emergence of the asexual zoospores, the species by minor details of size in the reproductive organs.

In nature these Fungi grow chiefly on decaying plant remains lying at the bottom of ponds and slow-flowing streams, or on humus in soils. Recent work seems to indicate that while some species of *Saprolegnia* occur regularly in water, others are more typically soil-inhabiting organisms living on humus. Many of these species occur in water only as a result of their reproductive bodies being washed out of the soil by the rain ; though if circumstances are favourable they will continue to develop under aquatic conditions. The name " Water Moulds," which is collectively given to this group, is therefore somewhat of a misnomer. They are generally obtained in the laboratory by placing dead flies or the cut seeds of hemp or cress in pond water, when, after a few days, a copious growth of the Fungus will appear on the bait. The Fungus produces a transparent whitish film over the substratum, which consists of a large number of very fine **hyphae,** collectively spoken of as the **mycelium.** These hyphae are very long and are not divided by septa into separate cells, hence they must be regarded as **coenocytic.** Only the sex organs are cut off by septa. The hyphae may be branched or simple, and the degree of branching varies very much among different species, and according to the conditions under which the Fungus is growing. In fact, not only the appearance but the whole sequence of events which make up the life history of *Saprolegnia* can be considerably altered according to the environmental conditions.

Saprolegnia grows rapidly, and under favourable circumstances asexual reproduction occurs within a few days of the appearance of the Fungus on the substratum. After a few days of active asexual reproduction the sex organs appear, and this is followed by a falling off in the formation of asexual bodies.

ASEXUAL REPRODUCTION

The asexual reproductive organs are **zoosporangia,** which are produced terminally at the ends of the hyphae (Fig. 200). They are long tubular structures, tapering at the tip. The contents become very dense as protoplasm migrates from the hypha towards the tip. Finally the structure is cut off at its base by a septum. Then the contents divide up into a large number of uninucleated **zoospores** (Fig. 201), each of which is pear-shaped and provided with a pair of apical flagella. When mature they escape one after another through an opening in the top of the sporangium. They swim away, but their activity is of brief duration, for after a short while they withdraw their flagella and become spherical. After a period of rest they again become active, only this time the cells are kidney-shaped and are provided with two lateral flagella. This phenomenon, consisting of two motile stages

FIG. 200.—*Saprolegnia ferax.* Formation of terminal zoosporangia.

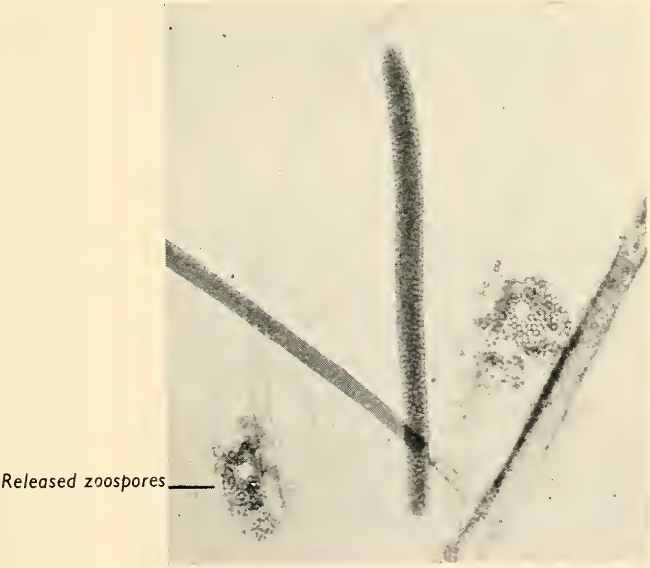

FIG. 201.—*Saprolegnia monoica.* Mature zoosporangium and discharged zoospores.

separated by a resting stage, is spoken of as **diplanetism.** The kidney-shaped zoospores, after a further period of activity, settle down and germinate into fresh hyphae. The second motile phase may be repeated more than once.

Although the behaviour in the genus *Saprolegnia* shows the true picture of diplanetism the conditions in allied genera are somewhat different, and since they are often encountered mixed with *Saprolegnia* it will be necessary to say something about them (Fig. 202).

In the genus *Achlya* the zoospores, instead of being discharged from the zoosporangium in a series, like bullets from a machine gun, are ejected in a cluster, forming a large mass around the apex of the zoosporangium. Here they immediately encyst and lose their flagella, thus passing into the second phase of a diplanetic condition. After a rest of several hours they emerge with reniform bodies and swim away with lateral flagella.

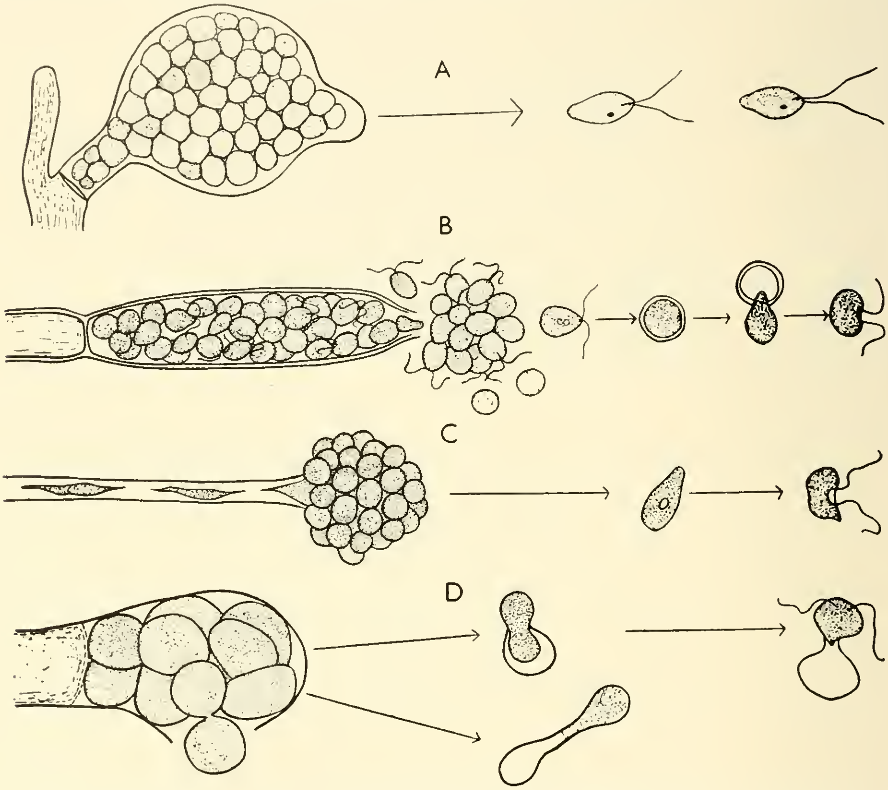

FIG. 202.—Different modes of discharge and further development of zoospores in Saprolegniaceae. A, *Pythiopsis*. B, *Saprolegnia*. C, *Aphanomyces*. D, *Thraustotheca*.

In the genus *Dictyuchus*, which may also be found in hemp-seed cultures, the zoospores are so closely packed in the zoosporangium that they assume a hexagonal pattern. In this genus they do not emerge through an apical pore but by numerous pores all over the surface of the sporangium. They are kidney-shaped with lateral flagella. Thus in this genus the encysted stage is passed through within the zoosporangium.

In the genus *Thraustotheca* the condition is somewhat similar, except that the spores are liberated by the breakdown of the wall of the sporangium in a non-motile spherical state and soon become reniform with lateral flagella.

Finally, in the genus *Aplanes*, a less common one, there is no motile stage at all, and the spores germinate within the zoosporangium by means of germ tubes which penetrate the wall of the sporangium and reach the exterior.

As will be seen in subsequent examples, there appears to be a progressive tendency among these groups of Phycomycetes to change from a condition with apically flagellate pyriform zoospores to one of reniform laterally flagellate zoospores. This is brought about by the interpolation of an encysted condition. In the more advanced types the production of the first type of zoospore disappears completely, and the second stage takes place within the sporangium, or in a vesicle formed as an outgrowth from it, so that the only motile stage is the third. Finally we see that this motility is lost and the spores germinate by a germ tube within the sporangium.

In *Saprolegnia*, after the liberation of the zoospores from the zoosporangium, secondary sporangia may be developed. This may be effected, either by the development of a second sporangium from the base within the primary one, or by the production of a hypha from the same point, which grows up through the opening in the tip of the primary sporangium to form a secondary sporangium, sometimes some way above the first. This is termed **proliferation.** Several successive generations of zoosporangia may be formed in this way (Fig. 203).

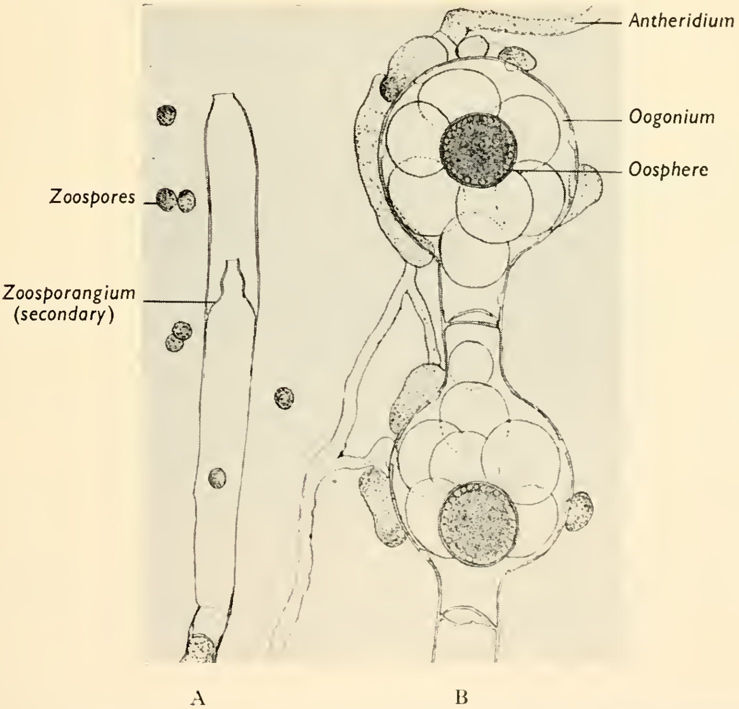

Fig. 203.—*Saprolegnia diclina.* A, Zoosporangium showing the development of a second zoosporangium inside the old one. Zoospores are escaping from the young zoosporangium. B, Sexual reproduction. Oogonia in chains with antheridia originating from different mycelium from the oogonia; the diclinous condition.

In addition to true asexual reproduction most species are capable of producing vegetative reproductive bodies termed **gemmae** which are developed from the tips of the hyphae. They are unicellular bodies, of varying shape, often globose or ovoid, but occasionally quite irregular. They are provided with dense protoplasm and stored food material, and are detached when mature. They germinate by the formation of a hypha which grows into a fresh mycelium. Little is known about the conditions which favour the production of gemmae, but they are partly hereditary, as it is not uncommon to find cultures which persist in forming these structures to the exclusion of any other type of reproductive body.

Sexual Reproduction

The sex organs consist of **oogonia** and **antheridia** (Fig. 203). The oogonia are borne at the ends of long hyphae, or laterally on short branches, or are occasionally intercalary. They arise in the same way as the zoosporangia, by the contents of the hyphae migrating into the tip, after which it is cut off by a septum. The oogonia are generally spherical. The wall of the oogonium is usually smooth but provided with pits, though in some species it is covered with spines or **papillae.** The contents of the oogonium divide up into a varying number of parts. Rarely one **oosphere** is formed, but in most species from two to as many as a hundred oospheres may be produced within the oogonium (Fig. 204). These oospheres are spherical and dark in colour, being richly supplied with oil, which serves as a food reserve. This oil is at first found as tiny droplets which coalesce to form a single drop which may either lie in the centre of the oosphere (**centric**), or may lie to one side of the oosphere (**excentric**). The oogonium is at first multinucleate and has dense cytoplasm. A central vacuole develops and the cytoplasm and nuclei are pushed out to the periphery, where the nuclei undergo a single mitosis and the majority of the daughter nuclei degenerate. Oospheres now form by the concentration of the cytoplasm around the remaining nuclei, each oosphere enclosing one nucleus (Fig. 205).

The antheridia may arise either from the same branch as the oogonia, in which case they are said to be **androgynous,** or from entirely different hyphae, when they are termed **diclinous** (Fig. 204). The antheridium is a narrow tube containing a rich supply of protoplasm, and is divided from its hypha by a septum ; frequently it may be profusely branched.

It grows towards the oogonium, and finally becomes closely adpressed, laterally, against its wall. A very fine outgrowth of the antheridium, the **fertilization tube,** penetrates the wall of the oogonium, generally through a pit, and makes its way to an oosphere. Each oosphere is fertilized by a different antheridium or by a separate branch from the same one. The contents of the antheridium pass into the oosphere through this fertilization tube, and the male and female nuclei fuse. A thick wall is secreted around each oosphere, which thus becomes an **oospore** (Fig. 207). The oospores are liberated by the breakdown of the oogonium. It seems probable in the case of oogonia with many oospheres that not all of them become fertilized.

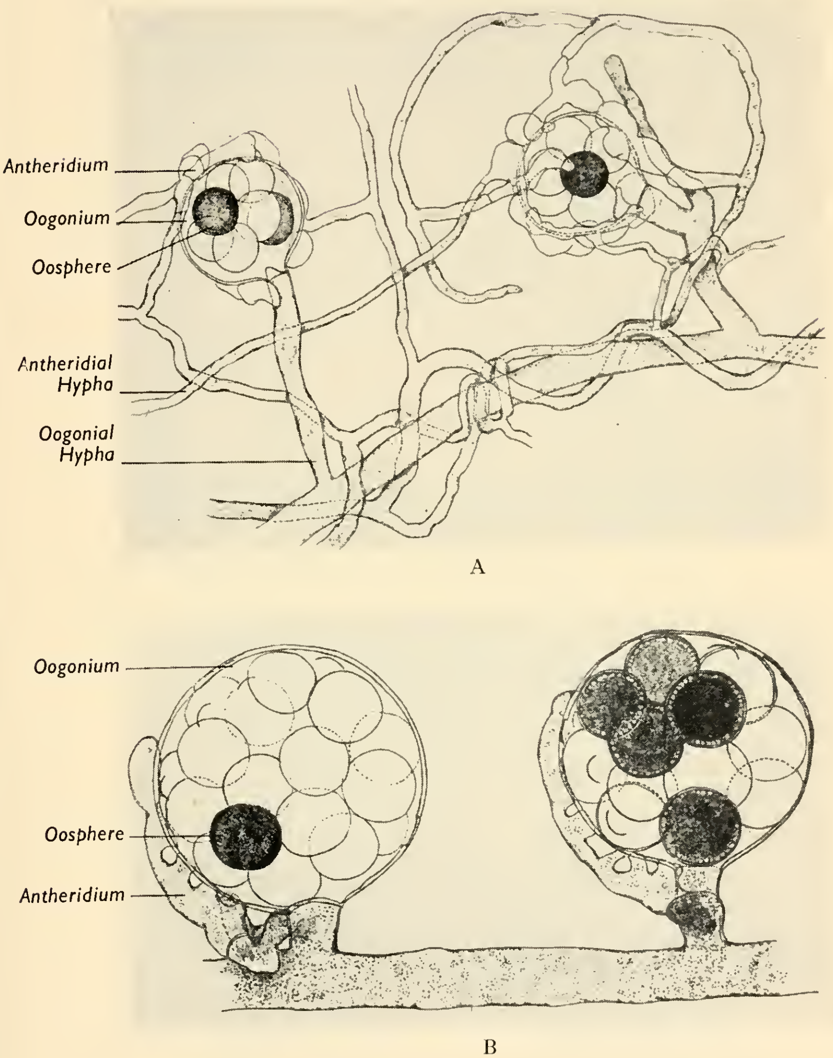

FIG. 204.—Comparison of antheridial origins. A, *Saprolegnia dioica*. Diclinous type with oogonia arising from stout hyphae, antheridia from thin ones. B, *Saprolegnia monoica*, androgynous type with antheridia arising from the stalks of the oogonia.

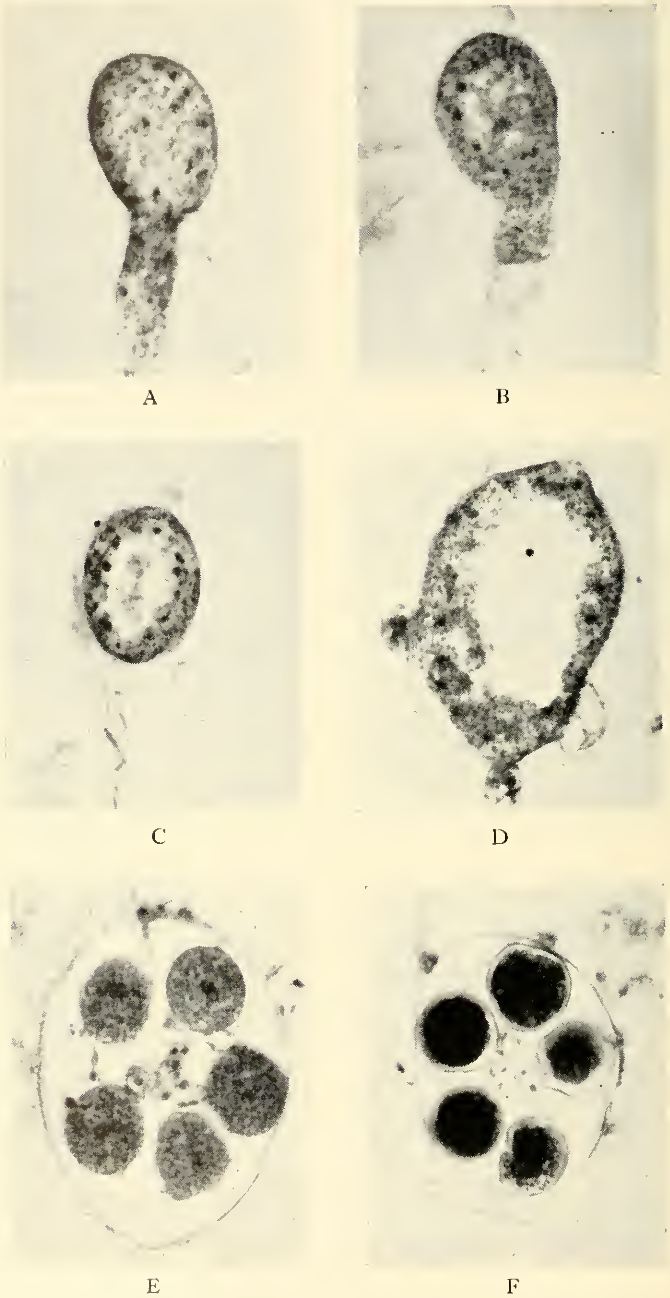

FIG. 205.—*Saprolegnia diclina.* Development of oogonium. A, Early stage, terminal swelling of hypha. B, Formation of basal septum. C, Development of central vacuole. D, Mitosis in peripheral protoplasm. E, Differentiation of oospheres. F, Oospores.

(*From preparations by the late Professor Trow.*)

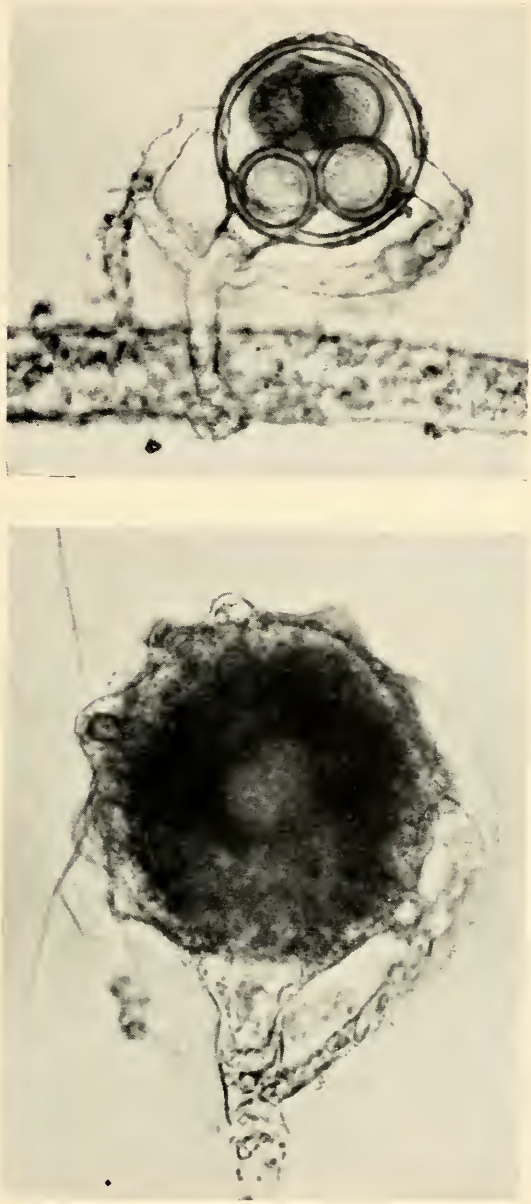

FIG. 206.—*Achlya racemosa.* Oogonium with smooth wall bearing two antheridia on the stalk of the oogonium. Below—*Achlya colorata.* Oogonium with spiny wall bearing one antheridium on the stalk of the oogonium.

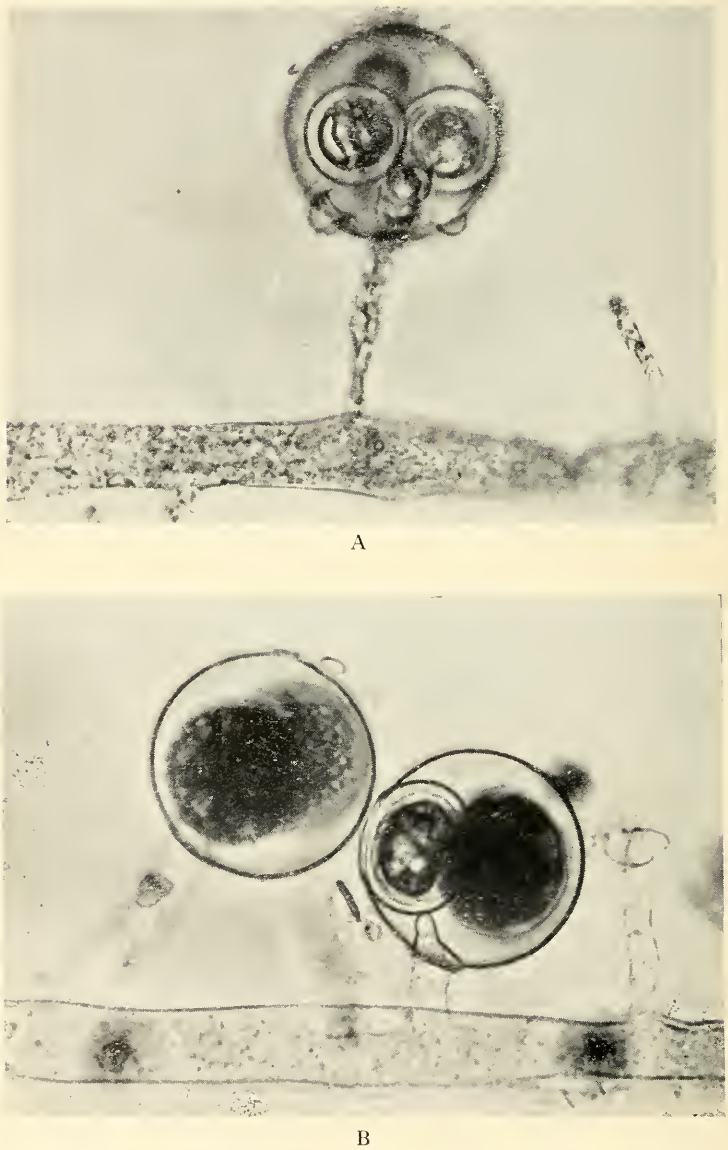

Fig. 207.—*Achlya caroliniana.* A, Single oogonium containing several mature oospores and remains of antheridium attached to its wall. B, Two oogonia, that on the left containing oospheres ; that on the right containing mature oospores.

Since it is very rare to find any oospheres lying among mature oospores it seems likely that those which fail to be fertilized develop parthenogenetically. In any case it is well known that in many species antheridia are either only rarely developed or not at all. In such instances, parthenogenetic development of the oospheres appears to be the rule. The oospore germinates by the formation of a germ tube which eventually produces fresh zoosporangia.

With one or two exceptions all the species of *Saprolegnia* are saprophytes on dead organic material, but *Saprolegnia parasitica* lives as a parasite on the gills of fish, causing the well-known Salmon Disease. This disease frequently attacks goldfish kept under unfavourable conditions in small tanks. It has been recently shown that excess of Calcium in the water favours the development of the fungus and makes the fish more liable to attack.

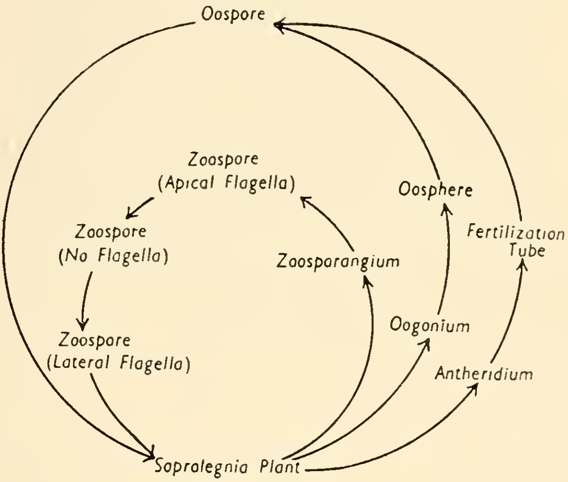

FIG. 208.—Life-cycle of *Saprolegnia*.

Monoblepharidales

The Monoblepharidales are saprophytic Phycomycetes which live submerged in fresh water on undecorticated twigs. The hyphae are filamentous and coenocytic. The protoplasm forms an extremely regular network which makes them easily recognizable. Rhizoids pass into the substrate upon which the Fungi live, and through them food material is presumably absorbed. The vegetative mycelium is sparsely branched, is rigid and possesses no septa, except in relation to the reproductive organs.

Asexual reproduction is by zoospores produced in filamentous terminal zoosporangia. The zoospores possess a single posterior flagellum. Sexual reproduction is oogamous. The antheridia produce motile antherozoids with a single posterior flagellum. The oogonium produces a single oosphere which is non-motile. The result of fertilization is a thick-walled, golden-brown oospore.

The order is a small one with a single family, the Monoblepharidaceae, which contains only one important genus, *Monoblepharis*.

Monoblepharis

It is not proposed to describe in detail any one species, since none is relatively more common than the others and there are differences in the sexual reproduction features which make a single description incomplete.

Until quite recently species of *Monoblepharis* were regarded as extremely rare Fungi and little was known about their life-histories. From the time when they were first described by Cornu over seventy years ago particular interest has attached to them because they are the only oogamous Fungi known in which a motile male gamete is employed. Recent work on the group has shown that the reason for their apparent scarcity was primarily a matter of understanding the rather peculiar requirements necessary for their active growth, without which they are usually swamped by more vigorous members of the Saprolegniaceae. It is desirable here briefly to indicate these conditions.

The Fungus favours the shallower parts of fresh-water ponds and ditches which are not liable to disturbance, resulting in the deposition of silt. Many and various are the submerged twigs upon which the Fungus will grow, and the host plant appears to have little influence upon the growth of *Monoblepharis*. When collected such twigs are not likely to show any obvious signs of the presence of the Fungus, but after being washed in water in the laboratory they are placed in glass jars filled half-full of sterile water. The jars are then placed for several weeks in a refrigerator working a few degrees above freezing-point, at the end of which time a copious growth of the Fungus may be expected.

From this fact it may be deduced that the Fungus grows best during the autumn months when the temperature is low and when other aquatic Fungi are less vigorous, and passes the spring and summer in a resting condition, probably in the form of the oospores.

On a well-infected twig the mycelium will appear pale grey in colour, forming a tuft of hyphae about 2 mm. in length. These hyphae are easily recognizable by the regular vacuolation of the protoplasm which gives the coenocytes a net-like appearance. Branching is monopodial and occurs rarely.

ASEXUAL REPRODUCTION

Under favourable conditions, that is between 8° and 12° C., asexual reproduction occurs. The **zoosporangia** arise as slightly swollen terminal portions of hyphae (Fig. 209). They possess at first a homogeneous cytoplasm and many nuclei, and are separated from the rest of the hypha by a septum. By means of cleavage furrows the contents become divided up into uninucleated zoospores. The apex of the zoosporangium dissolves away and the spores creep out by amoeboid movement. These zoospores, even at this stage, possess a single flagellum, three or four times as long as the diameter of the spores, and either immediately, or after a period of amoeboid movement, each swims away. Zoospores may frequently fail to gain the outside of the zoosporangium, but even under such conditions they germinate, producing a single hypha from which a fresh mycelium is formed eventually.

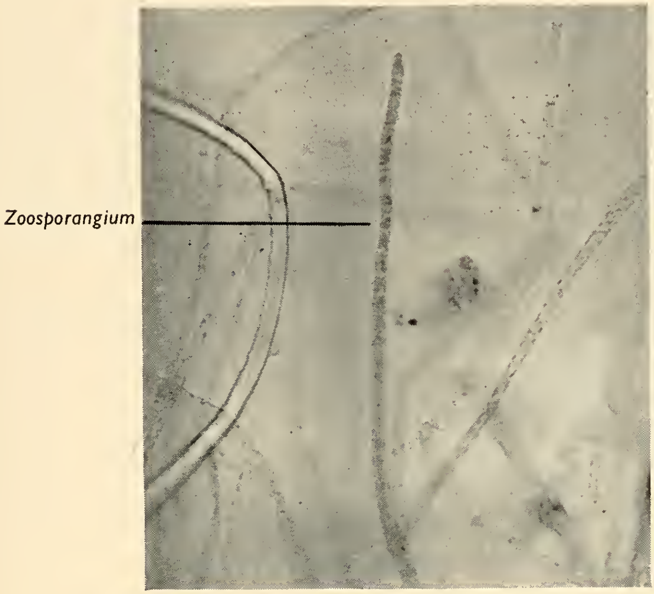

FIG. 209.—*Monoblepharis sphaerica*. Zoosporangium.

SEXUAL REPRODUCTION

Sexual reproduction is favoured either by warm conditions or by freezing. The process differs somewhat in the species, firstly in the relative positions of the antheridia and oogonia, and secondly in the position where the oospore matures.

In some species, *e.g.*, *Monoblepharis polymorpha*, *M. insignis*, *M. fasciculata* and *M. sp. nov.*,* the antheridium appears to be inserted on the oogonium, but a study of their development shows that in reality the oogonium is formed beneath a terminal antheridium, although as the oogonium matures the antheridium becomes pushed to one side. In others, *e.g.*, *Monoblepharis sphaerica* and *M. hypogyna*, the antheridium may develop below the oogonium.

THE ANTHERIDIUM

The **antheridium** is an oval structure cut off by a septum and is from the first multinucleate. The cytoplasm is homogeneous and when mature is divided transversely into from four to eight uninucleate **antherozoids.** A small opening appears in the apex of the antheridium, and towards this the antherozoids crawl by amoeboid motion, each trailing its single long flagellum

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* This species, not yet described, is illustrated in Fig. 211.

behind it. In shape these antherozoids resemble the zoospores, but they are smaller and their amoeboid movement is more pronounced.

THE OOGONIUM

After the antheridium has been cut off by a septum, the proximal portion of the hypha below the septum becomes distended and forms a lateral projection, which finally enlarges into a clavate body which is also cut off by a cross wall. The **oogonium** gradually becomes more rounded in shape. The contents then move away from the wall, forming a central spherical oosphere.

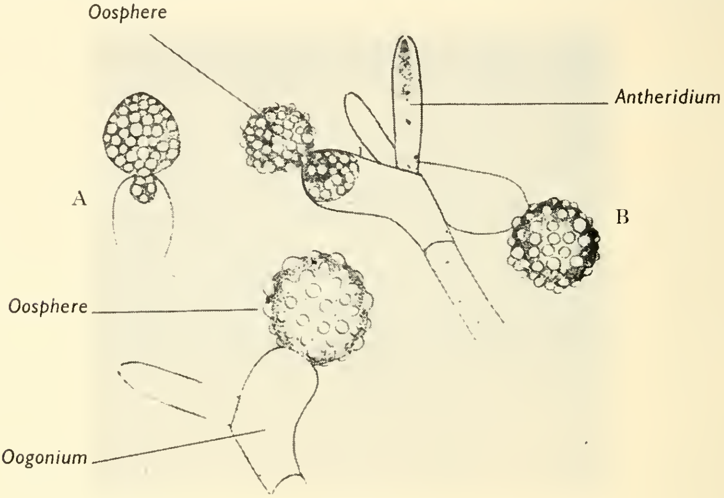

FIG. 210.—*Monoblepharis polymorpha.* Stages in the development of the oospore. A, Extrusion of the oosphere. B, Liberation of antherozoids. C, Mature oospore.

In certain species the oogonium is formed terminally at the end of the hypha, and after it has been separated by a septum the portion of the hypha below forms a lateral projection which grows out as an hypogynous antheridium. In one species, *Monoblepharis macrandra*, the oogonium and antheridium occupy terminal positions on separate hyphal branches. In this case, as growth continues, additional antheridia or oogonia may develop below the terminal ones, which therefore appear to be produced in chains.

When the oosphere is mature the oogonium opens at the top to allow entry for the antherozoid, and mucus is secreted through the opening by means of which the antherozoid becomes attached and its union with the oosphere follows immediately (Fig. 210).

THE OOSPORE

The genus *Monoblepharis* is sometimes divided into two sub-genera which are distinguished by whether the **oospore** develops within the oogonium (Fig. 211) or whether it leaves the oogonium immediately after fertilization and completes its maturation outside the mouth of the oogonium. In either case a thick golden-brown wall quickly develops around the zygote, forming a very conspicuous structure. The oospore may either remain attached to the oogonium for a considerable time or it may be shed soon after fertilization (Fig. 212). It germinates, usually after a period of rest, to produce a hypha from which a new mycelium will be formed.

FIG. 211.—*Monoblepharis sp. nov.* Group of oogonia with smooth endogenous oospores.

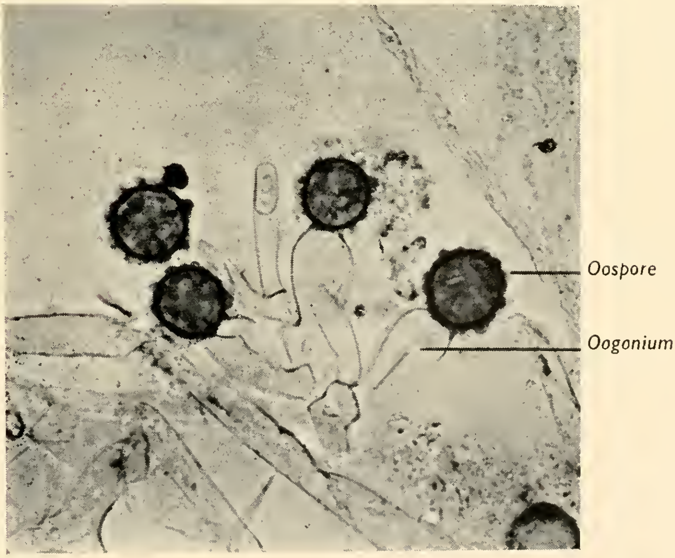

FIG. 212.—*Monoblepharis polymorpha.* Group of oogonia with spiny exogenous oospores.

RELATIONSHIPS

The chief interest of the Monoblepharidales lies in the fact that they are the only group of Phycomycetes, or in fact of the Fungi, in which a relatively large non-flagellate oosphere is fertilized by a small motile, flagellated antherozoid. By those who would relate the Phycomycetes directly with the Algae, this group is used to point out a close similarity to the Chlorophyceae, and in particular to *Vaucheria* and *Oedogonium*. On the other hand, those who maintain that the higher Phycomycetes are derived from simpler isogamous Chytridiales see in the antherozoid a similarity to the isogamous gamete of a type like *Rhizophidium*, pointing out at the same time that its amoeboid character is also a primitive feature. Similarly they consider that in the oogonium and oosphere there is a connecting link with the Saprolegniales and Peronosporales. While the possibility of an algal relationship is certainly attractive, it must be admitted that most mycologists now consider the latter view is more probable.

Peronosporales

The Peronosporales are Phycomycetes in which the vegetative mycelium is composed of branched coenocytic hyphae, septa occurring rarely in older hyphae or in the formation of the sex organs. Sexual reproduction is oogamous, but only one oosphere is formed in each oogonium. Fertilization is effected by a fertilization tube. Asexual reproduction may be by sporangia, which either give rise to zoospores or produce spores which germinate by a germ tube. In the higher members conidiophores are produced which abstrict conidiospores, which also germinate directly by a germ tube. Intermediate stages between the two types are known. Where zoosporangia are produced the contents pass out into a vesicle in an incompletely differentiated state and then divide into reniform zoospores with lateral flagella.

The species are characteristically parasitic on higher plants, though a few occur as parasites of Thallophytes. Some can live as saprophytes after the death of the host, but in the higher members this faculty is absent, nor can they be cultivated on artificial media.

We shall consider three examples of this order, *Pythium*, *Cystopus* and *Peronospora*, each of which represents a separate family and shows an apparent advance on the previous one in adaptation to a land habit.

Pythium debaryanum (The "Damping-off" Fungus)

Unlike *Saprolegnia*, *Pythium debaryanum* can live as a parasite within the tissues of seedlings, causing them to collapse and producing a disease which is frequently spoken of as "damping-off" (Fig. 213). During the early stages in the growth of the Fungus no external signs of its presence are noticeable on the host, and it is only after it has gained a firm hold that the hypocotyl collapses, with the appearance of having been pinched off near the base. With the death of the host the Fungus continues to live saprophytically upon the dead remains, and by means of external hyphae and zoospores attacks other seedlings near by. The disease spreads rapidly, and in a comparatively short time large numbers of seedling plants are killed. *Pythium debaryanum* also lives as a saprophyte in the soil, remaining there indefinitely before once again becoming parasitic on some higher plant. It should be noted that many other species of *Pythium* also cause disease among higher plants.

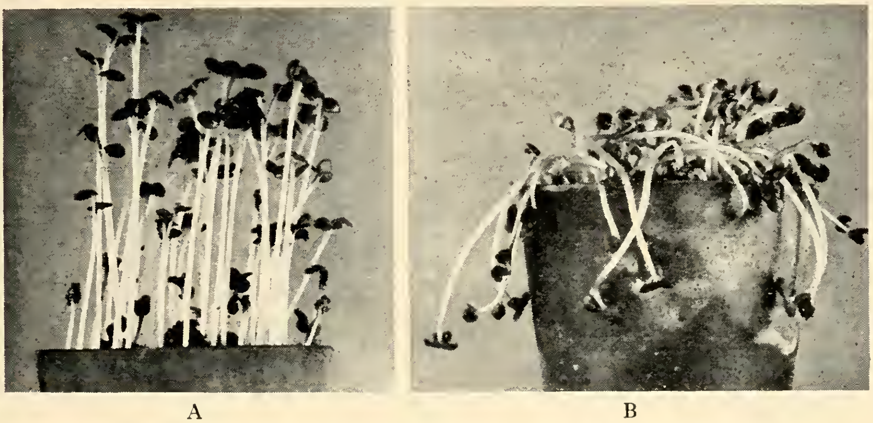

FIG. 213.—*Pythium debaryanum* on seedlings. A, Normal seedlings. B, Seedlings showing "Damping-off."

Pythium consists of long branched **coenocytic hyphae,** transverse septa being absent, except in association with the sex organs. The contents of the hyphae consist of a vacuolated mass of protoplasm in which nuclei are embedded. The infecting hypha may find its way into the host through a stoma, or may gain an entrance by dissolving the cell wall, probably by enzyme action. Once inside it grows rapidly, branching and forming an extensive **mycelium.** Although for the most part the hyphae remain in the intercellular spaces of the stem, they have the power of penetrating into the cells. Usually the mycelium is restricted, at any rate in the early stages of the disease, to the cortical region of the hypocotyl just above soil level ; the cells of the host die and collapse at this point and the seedling falls over. Later the hyphae make their way into the vascular bundles, where they absorb food substances which are being carried to different parts of the plant. It is the appropriation of this food and the formation of waste products by the Fungus which lead to the death of the host and so cause the Fungus to become saprophytic. Long before the death of the seedling, however, reproductive organs are developed. Reproduction may be either by asexual or sexual methods.

ASEXUAL REPRODUCTION

The asexual reproductive organs are formed almost exclusively on aerial hyphae. Such hyphae are produced from a mycelium which grows out from inside the host, in the presence of a damp atmosphere, which favours growth of the Fungus and also the production of zoospores. The tip of a hypha swells up and develops into a **zoosporangium,** which is then cut off by a septum (Fig. 214). When the zoosporangium is mature a papilla is formed either at the apex or from the side of the sporangium. It is at first tubular, but later swells out at its distal end to form a vesicle. Into this the contents of the sporangium pass in a partly differentiated state, and in the papilla **zoospores** are formed. They are reniform with two lateral flagella. The vesicle then breaks and the zoospores swim away in the water film. It sometimes happens that the sporangium functions as a **conidiospore,** and instead of forming zoospores grows out directly into a **germ tube** which produces a new hypha. In this way a new mycelium develops without the intervention of swimming spores. This provision enables reproduction to take place under relatively dry conditions where there is insufficient moisture for zoospores to swim in.

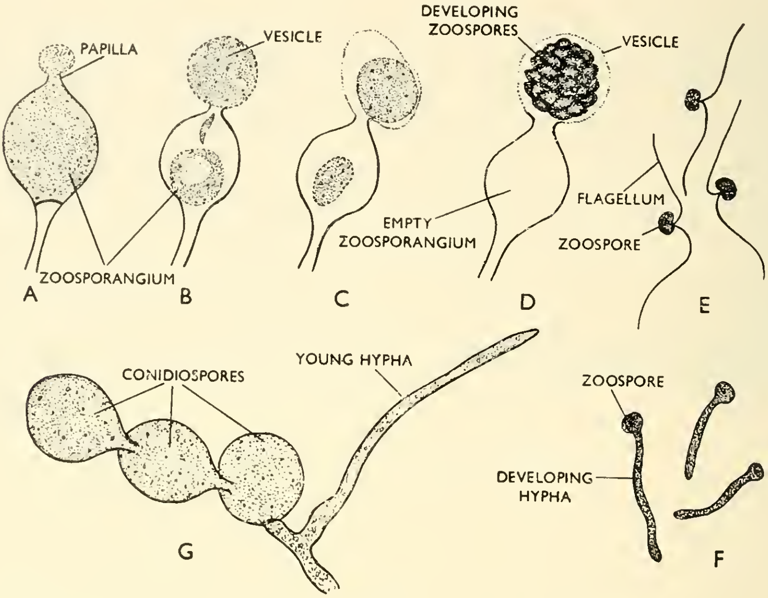

Fig. 214.—*Pythium.* Asexual reproduction. A to D, *Pythium carolinianum.* A, zoosporangium. B, Formation of vesicle. C, Migration of the cytoplasm into the vesicle. D, Differentiation of zoospores. E, Zoospores. F, *Pythium proliferum.* Germination of zoospores. G, *Pythium intermedium.* Formation of conidiospores.

Sexual Reproduction

The sex organs are developed within the tissues of the host, and consist of **antheridia** and **oogonia** (Fig. 215). They appear at a late stage in the life-history of the Fungus, when the food material of the host is nearly exhausted. The oogonium is developed from the tip of a hypha into which some of the protoplasm, together with a number of nuclei, migrate and are cut off by a septum. The tip now becomes swollen, and the protoplasm separates into a central granular portion, the **oosphere**, and a peripheral layer, the **periplasm**.

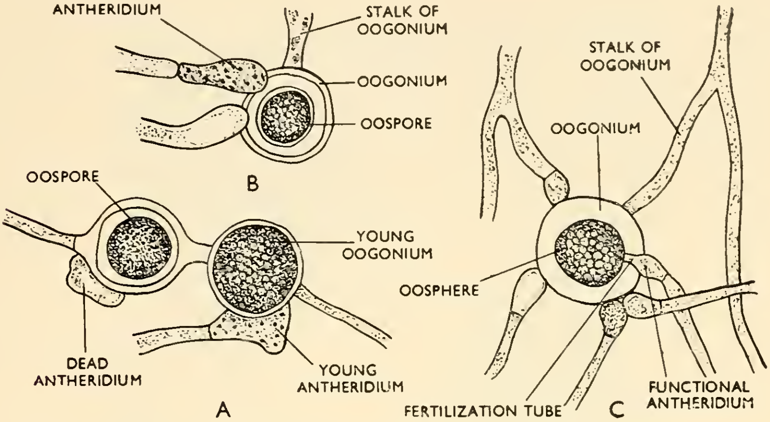

Fig. 215.—*Pythium debaryanum.* Sexual reproduction. A, Young oogonium with antheridium attached before the formation of the fertilization tube; mature oospore on left. B, Mature oogonium with oospore and disorganizing antheridium. C, Oogonium with oosphere inside and several antheridia attached, one with fertilization tube passing from the antheridium through the oogonium into the oosphere.

All except one of the included nuclei migrate to the periphery and abort, so that only one functional female nucleus remains in the centre (Fig. 216).

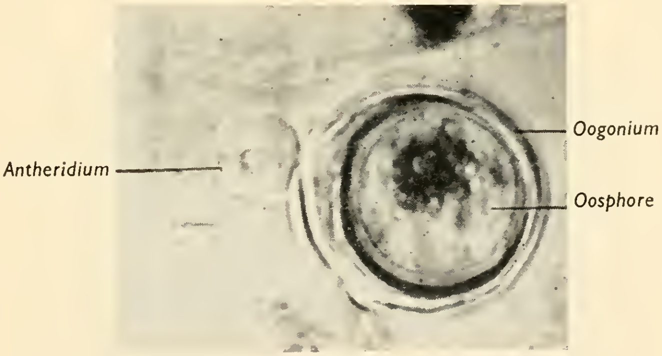

Fig. 216.—*Pythium debaryanum.* Smooth oogonium with single oospore and attached antheridium.

Meanwhile the antheridium is developed as a club-shaped branch, either on the same or on an adjacent hypha, and is also cut off by a transverse wall (Fig. 215). The antheridium now elongates, its tip comes into contact with the wall of the oogonium, which it dissolves at this point, and a **fertilization tube** is formed which penetrates the oogonium and passes into the oosphere. It is probable that only a single male nucleus enters the oogonium, and this immediately fuses with the female nucleus. The fertilized oogonium secretes a thick wall round itself, and thus becomes an **oospore** (Fig. 217). In the oospore are a large number of oil globules which constitute the food reserve of the zygote. The oospore is a drought-resisting structure, associated with the dessication which the Fungus may experience. The germination of the oospore only takes place in the presence of moisture and may be delayed

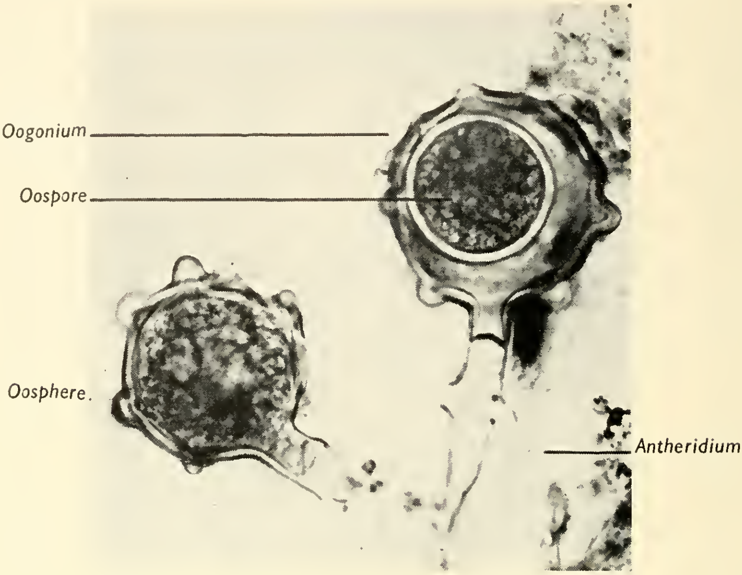

FIG. 217.—*Pythium proliferum.* Spiny oogonia with oosphere, left, and oospore, on right.

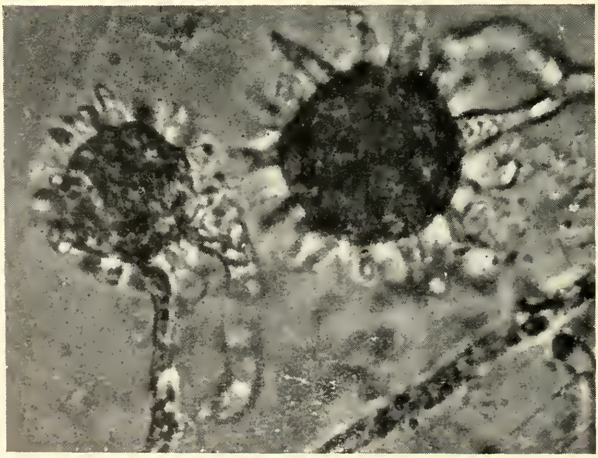

FIG. 218.—*Pythium mamillatum.* Spiny oogonia with androgynous production of antheridia.

almost indefinitely. The thick wall of the oospore bursts, and the contents, surrounded by a thin membrane, may either grow out directly into a hypha, which immediately forms a fresh mycelium, or, under other conditions, this hypha may bear an asexual sporangium. Occasionally, however, the development of the hypha is suppressed, and zoospores similar to those which would have been borne in an asexual sporangium are developed directly within the oospore. These swim about in the water surrounding the host, until they find fresh tissues to penetrate, when they form a germ tube which develops into a hypha.

The life-cycle of *Pythium* is graphically represented thus (Fig. 219):—

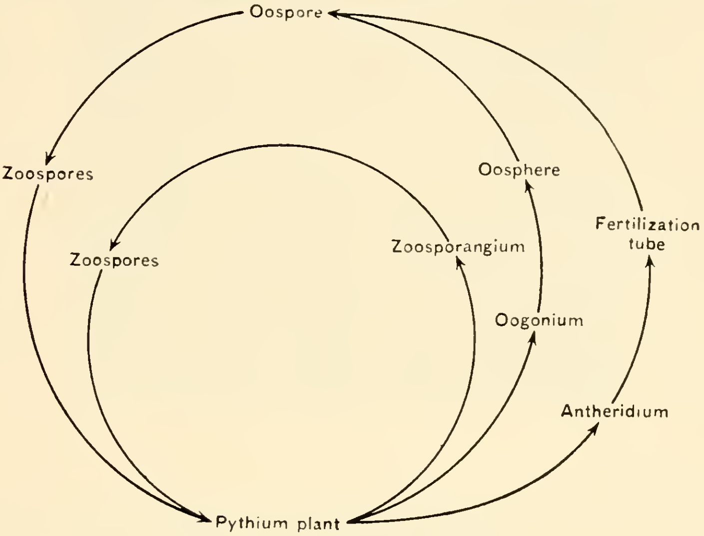

Fig. 219.—Life-cycle of *Pythium*.

It is important to realize that a large number of species of *Pythium* occur in this country, many of them in the soil, and that while some are destructive parasites of higher plants others may play an equally important part in the decomposition of plant remains in the soil. These species show a considerable variation from the type described above. For example, in some the oogonium may be beset with spines, while in others the chief differences are in the formation of the zoosporangia and the germination of the zoospores. In fact it is possible to trace certain evolutionary sequences indicating a possible gradual evolution from a typically aquatic mode of life to one adapted to terrestrial conditions among the various species of the genus. A similar sequence is found in the genus *Peronospora*, and we will postpone our account of these matters till after we have described the life-history of this organism.

Peronospora (The Downy Mildew)

There are a number of species of *Peronospora* which occur on higher plants, all of which cause diseases known as the Downy Mildews. Most of these species occur on distinct host plants and differ from one another only in minor particulars of the size of the spores. Recent investigations have tended to split up certain of the older species. Thus the well-known form *Peronospora parasitica*, which is widely distributed on Cruciferous plants, has been split up into a number of separate species. One of the commonest forms of this is *Peronospora cheiranthi*, which occurs on Wallflowers (Fig. 220).

It lives as an obligate parasite within the tissues of its host plant and spreads by means of a branched **mycelium,** which consists of **hyphae** that ramify between the cells of the host. These hyphae do not penetrate into the host cells but only pass between them. They give off, however, lateral branches which enter the cells of the host and inside form branched or swollen structures which are called **haustoria** (Fig. 221). These secrete enzymes, by the aid of which the protoplasm of the host cells is broken down and absorbed by the Fungus. Externally the Fungus causes a soft, white, downy appearance on the leaves of the host plant, often associated with twisting and stunting of the affected area.

Peronospora parasitica is commonly found on *Capsella bursa-pastoris* (Shepherd's Purse), frequently associated with *Cystopus candidus* (White Rust) (see p. 235). Other species are known to attack many crops of economic importance, such as beet, maize, tobacco and turnips. A Fungus which, like *Peronospora*, only attacks a specific host is said to exhibit **selective parasitism.**

Asexual Reproduction

Peronospora reproduces both asexually and sexually. The asexual reproduction shows an advance on the condition found in *Pythium*, in that the reproductive bodies are specially adapted for aerial distribution. The organs are termed **conidiophores,** on which are borne specialized **conidiospores** (Fig. 222). The conidiophores arise from the intercellular mycelium, emerge through the pores of the stomata, and become repeatedly and dichotomously branched. They may be to some extent septate. To the end of each of the branches there passes a single nucleus ; a swelling occurs, and into this the nucleus passes. The swelling increases until a spherical or oval spore is formed, attached to the conidiophore by a short thin stalk or **sterigma,** which is water soluble, a fact which facilitates distribution of the spores in damp weather.

Only a very small proportion of the conidiospores produced by the Fungus ever come to rest on a suitable substratum, *i.e.*, the leaf of another plant of the same species of host, under environmental conditions suitable for germination. The Fungus must therefore produce a very large number of spores on the chance that a few will find conditions where germination is possible. The presence of a water-soluble sterigma tends to ensure that spores shall only be shed in weather when the humidity is sufficiently high to render germination possible.

FIG. 220.—*Peronospora cheiranthi* attacking Wallflower.

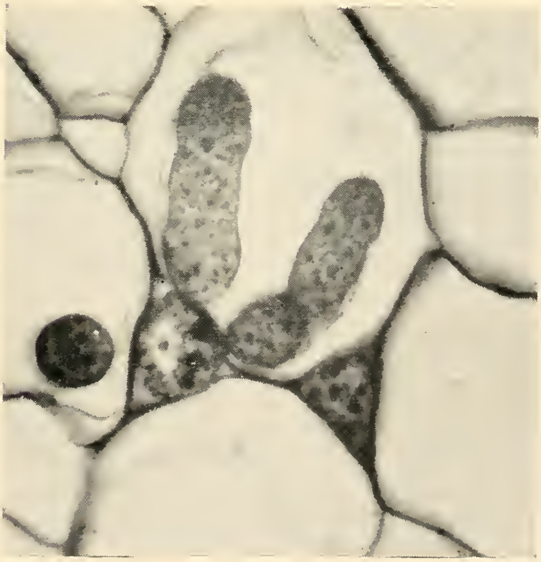

FIG. 221.—*Peronospora parasitica.* Haustoria in cell of host.

Under favourable conditions for germination the spore wall bursts and a germ tube is put out, which grows over the surface of the leaf until it comes to the pore of a stoma, when it immediately passes down into the leaf and forms the mycelium which, as we have already said, ramifies in the spaces between the cells. Considerable investigation has been directed to the problem of what induces the growth of the germ tube into the stomatal opening and the growth of the young conidiophore out of it at a later stage. Chemotropism and hydrotropism have both been suggested, but the true explanation is still a matter of some uncertainty.

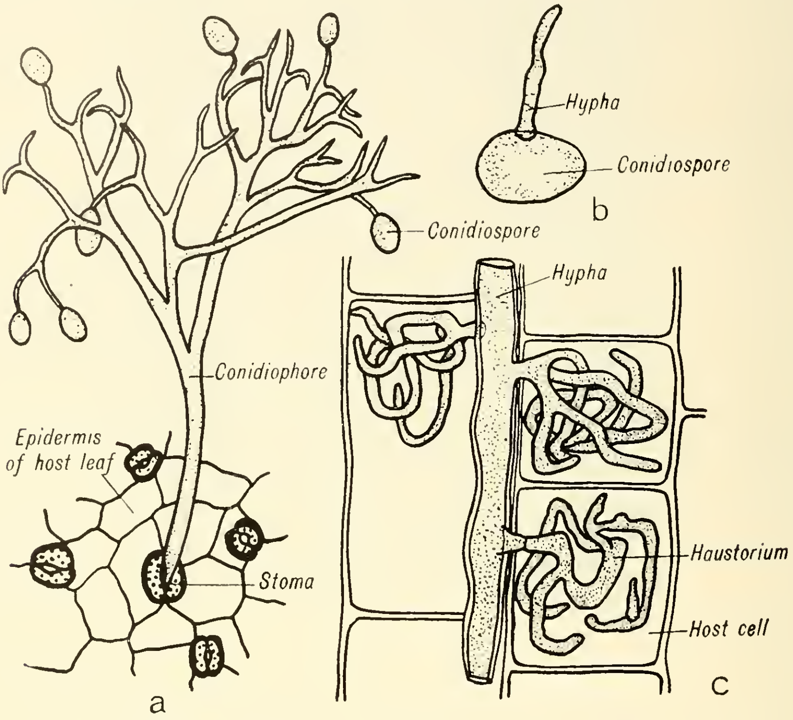

FIG. 222.—*Peronospora sp.* A, Branched conidiophore emerging from stoma. B, Germination of conidiospore. C, Mycelium in host tissue.

SEXUAL REPRODUCTION

Sexual reproduction is of an oogamous type, resembling in general that of *Pythium*. It takes place under conditions adverse to the Fungus and in the deeper layers of the host tissue, generally in the stem, and especially in the pith. The sex organs consist of **antheridia** and **oogonia,** and are formed terminally at the apices of either the same or of separate hyphae (Fig. 223). The oogonium is a swollen structure containing, at an early stage, a large quantity of cytoplasm and many nuclei. The antheridium is more tubular in shape, and it, too, is multinucleate.

As the oogonium swells a separation into a dense central **oosphere** and a less dense **periplasm** occurs, associated with changes in the position of the nuclei. Up to this stage they have been more or less evenly distributed through the oogonium, but with these changes in the cytoplasm one nucleus places itself centrally in the oosphere and functions as the female nucleus, while the rest pass into the periplasm and eventually abort. The antheridium now comes into contact with the oogonium, and a fine **fertilization tube** is formed which penetrates through the periplasm and discharges a single male nucleus, together with a small amount of cytoplasm, into the oosphere. Conjugation of male and female nuclei takes place and a zygote is formed. Fertilization stimulates the secretion of wall material which occurs in the periplasm. The precise way in which this takes place varies in different species. In general, it appears that within the oogonial wall a very thick wall is laid down, forming the wall of an **oospore** (Fig. 224), and enclosing the original oosphere. The periplasm may also contribute an **exospore** wall to the oospore.

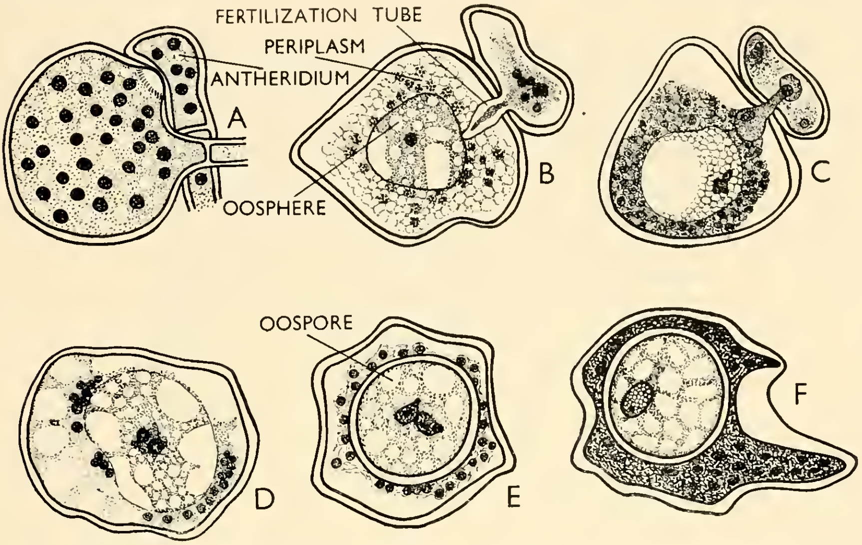

FIG. 223.—*Peronospora parasitica.* Sexual reproduction. A, Young oogonium with receptive papilla and antheridium. B, Oosphere and periplasm, antheridium with fertilization tube. C, Male nucleus passing through fertilization tube towards oosphere. D, Sexual nuclei paired in oosphere. E, Early stage in fusion of sexual nuclei. Oospore wall forming. Periplasm degenerating. F, Mature oospore with fusion nucleus. (*After Wager.*)

The oospore is a resting spore, remaining unchanged until the decay of the host tissues, and after that it may remain in the soil for some months before germination takes place. Under favourable conditions it germinates by the bursting of the wall and the development of a germ tube. In cases where the Fungus parasitizes an annual plant the oospore is the means whereby the Fungus passes the winter months after the death of the host, and germination takes place the following spring.

There is some doubt as to precisely where the reduction division occurs. Some authorities claim that it takes place during the multiplication of nuclei in the formation of the oogonium and antheridium, while according to others it occurs in the first division of the germinated oospore, and on the whole this latter view seems the more likely, on account of what is known of the nuclear behaviour in allied genera of Fungi.

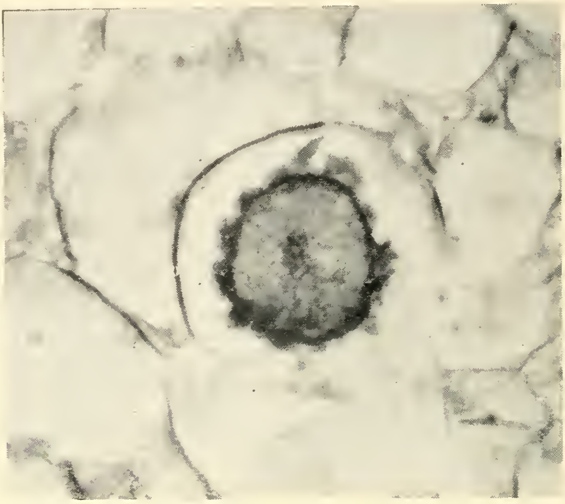

FIG. 224.—*Peronospora sp.* Mature oospore with rugose exospore in tissue cell.

The life-cycle of *Peronospora* may therefore be represented by the following diagram (Fig. 225) :—

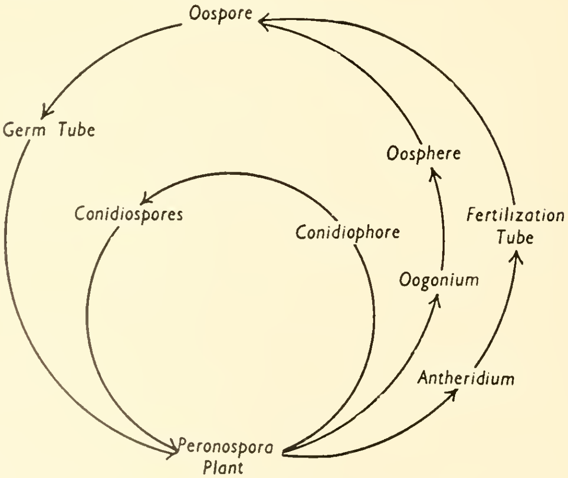

FIG. 225.—Life-cycle of *Peronospora*.

Control of Downy Mildew and other Mildews is generally effected by covering the plants with some substance which will kill the Fungus without damaging the host tissues. In recent years great advances have been made in the study of sprays and spraying machinery. Two chief types of sprays are employed, the one in which a substance or substances are dissolved in liquid and sprayed on to the foliage with the idea of covering the whole surface of the host with a film of the solution. The second is by the use of extremely fine powders which are blown over the plant, relying on the dampness of the leaves to retain them. In the former case a great proportion of the liquid is lost, and what is known as a " spreader " is now employed to increase adhesion of the spray to the leaves. This may take the form of an oil, the whole solution being worked up into an emulsion. Where Downy Mildews are concerned the solution known as **Bordeaux mixture** is generally employed. It consists of a dilute solution of copper sulphate and lime, sometimes with the addition of paraffin oil.

The Evolution of the Conidiospore

While it is obviously unwise to draw too rigid conclusions about the evolution of a structure from a study of a limited number of existing types, the genus *Pythium* provides a number of examples in which the asexual reproductive organs apparently show a transition from a simple zoosporangium to a true conidiospore (Fig. 226). It must be realized, however, that in citing the following species as stages in such a series the reproductive organs may in certain instances germinate by different methods under differing conditions, and that many species of *Pythium* exhibit both zoospores and conidiospores, the former being produced under wet and the latter under dry conditions.

In the genus *Phytophthora*, which is included in the family Pythiaceae, the zoosporangia develop from the vegetative mycelium and form zoospores which are kidney shaped and escape directly from the sporangium without the formation of a vesicle. Such a condition is not found in any species of *Pythium*, for this is one of the characters used to separate the genera. In *Pythium gracile*, however, the zoosporangia are filamentous and differ but little from the ordinary hyphae. Each, however, produces a long, narrow vesicle which terminates in a spherical swelling and resembles a zoosporangium in appearance. It is this swollen sporangium-like structure which grows out of the host cell and in which the zoospores are developed, and from which they are finally liberated as reniform, biflagellated bodies.

In *Pythium debaryanum*, as we have seen, the zoosporangia are spherical in shape and develop a vesicle into which the contents of the zoosporangium pass and in which the zoospores are differentiated. Under dry conditions, however, conidiospores are formed which are similar in shape and size to the zoosporangia. In fact, we may consider that these conidiospores are really zoosporangia which form no zoospores but germinate by a germ tube.

In *Pythium intermedium* both zoosporangia and conidiospores occur.

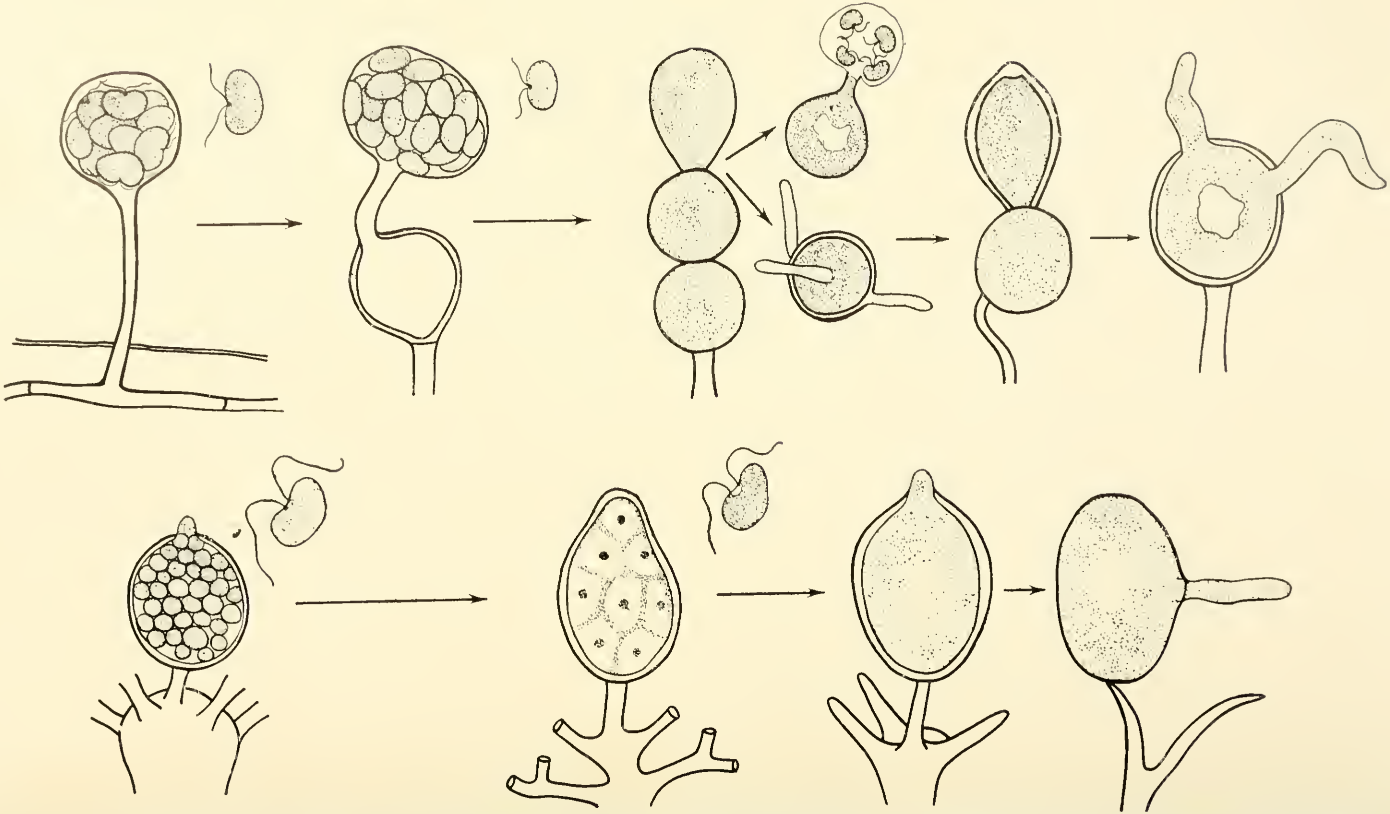

Fig. 226.—Comparative evolution of the conidiospore in Pythiaceae and Peronosporaceae. Equivalent stages are shown one above the other. Top line, from left to right: *Pythium gracile*, *Pythium debaryanum*, *Pythium intermedium*, *Pythium vexans*, *Pythium ultimum*. Bottom line, left to right: *Basidiophora entospora*, *Plasmopara nivea*, *Bremia lactucae*, *Peronospora parasitica*.

The latter germinate by one or more germ tubes, while the former produce zoospores in a vesicle. In both cases, however, these reproductive bodies are formed in chains so that the conidiospores appear to be abstricted in a similar way to the zoosporangia of *Cystopus*, but they do not give rise to zoospores as in that genus.

In *Pythium vexans* zoosporangia are rarely formed, but the asexual reproductive organs behave as conidiospores, the germ tube being produced in place of the papilla of a zoosporangium.

Finally in *Pythium ultimum* zoosporangia are never formed, but spherical terminal conidiospores are produced which germinate by a germ tube in the usual way.

A similar series can be traced in the genera which comprise the Peronosporaceae, and we may briefly outline the series here.

In the genus *Basidiophora* the sporangia are borne in clusters from the top of a clavate sporangiophore. Each zoosporangium is spherical and possesses a definite apical papilla through which biflagellated, reniform zoospores ultimately emerge.

In the genus *Plasmopara* the sporangiophore is complexly branched and the zoosporangia develop terminally on the ultimate branches. Usually the contents of the zoosporangium divide up into separate zoospores which escape, but sometimes the structure forms a germ tube and behaves as a conidiospore.

In the genus *Bremia* the sporangiophores are complexly branched, each branch terminating in a saucer-shaped expansion bearing a number of sterigmata. On each of these a single conidiospore is borne. This conidiospore possesses an apical papilla, and it is through this that the germ tube emerges. Zoospores are never formed.

Finally in the genus *Peronospora* itself the branched sporangiophores terminate in long, fine sterigmata, each of which bears a single conidiospore. There is no apical papilla, and the germ tube is produced from an indeterminate point on the side of the spore.

From the above evidence, therefore, it seems reasonable to consider that the conidiospore, at least in this group, has been derived from a zoosporangium, the contents of which produce a germ tube instead of dividing up into a number of separate zoospores. This change from motile zoospores to conidiospores may have been brought about as an adaptation to drier conditions in which motile zoospores were less successful than aerially distributed conidiospores.

Cystopus candidus (Albugo candida) (The White Rust of Crucifers)

This Fungus attacks all kinds of cruciferous plants and may sometimes cause swelling and twisting of the stems, especially in young plants. The disease is easily recognizable by the white, smooth, glossy patches which gradually turn powdery and give the Fungus its common name of White Rust (Fig. 227).

The fungal **mycelium** is intercellular, like that of *Peronospora*, and sends **haustoria** into the cells of the host plant ; these haustoria are fairly well developed and end in button-like projections in the host cells. It is through them alone that the Fungus obtains its nourishment. It spreads rapidly within the host and may attack all parts of the plant, besides those where the white patches are apparent. Reproduction is both sexual and asexual, though there is no alternation of generations.

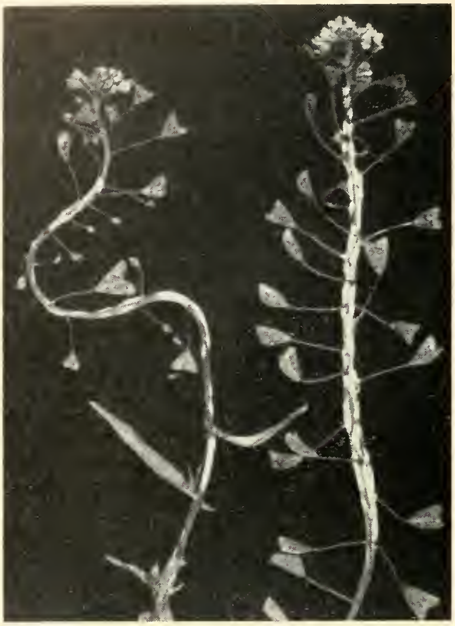

Fig. 227.—*Cystopus candidus* on *Capsella* showing white pustules and distortion of the stem.

Asexual Reproduction

The asexual reproductive organs are developed just below the epidermis of the stem or leaf of the host plant. In this position short **sporangiophores** are produced in compact groups, forming an almost complete tissue. As growth continues a nucleus passes to the tip of each sporangiophore, and this is followed by a deepening constriction around the tip, thus cutting off a **zoosporangium** with one nucleus. Immediately behind, another zoosporangium is cut off in the same way, until chains of sporangia have been formed, one above the other, from each sporangiophore (Fig. 228). The outer layer of the wall of the sporangium becomes gelatinous, and as a result the sporangia tend to stick to one another.

The growing pressure of all these zoosporangia cut off below the epidermis finally causes it to lift up, then to split and break up, exposing the white sporangia. It is interesting to note that during the development of the sporangia they are protected by the host epidermis, which is only ruptured when at last the distal sporangia are mature.

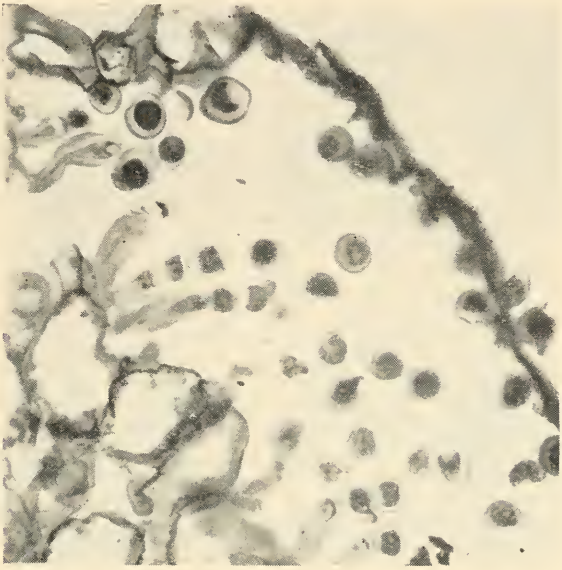

FIG. 228.—*Cystopus candidus.* Section through stem of host showing sporangiophores and abstricted zoosporangia covered by the remains of the epidermis.

The zoosporangia are finally liberated and disseminated by the wind, and when conditions are favourable, that is, when the atmosphere is damp, they germinate by producing a number of **zoospores** (Fig. 229) in each zoosporangium. These zoospores are kidney-shaped with two laterally placed flagella. From these zoospores fresh infections of host plants are derived.

It is sometimes stated that *Cystopus* reproduces asexually by means of conidiospores. According to this view the sporangiophore is regarded as a conidiophore, from the tip of which conidiospores are abstricted in acropetal succession, in a way similar to that found in many Fungi, *e.g*, *Aspergillus.* It is certainly true that the method of abstriction of the zoosporangia in *Cystopus* is effected in much the same way. The difference lies in the method of germination of these zoosporangia. The typical conidiospore germinates by means of a germ tube and thus forms a hypha directly, one hypha being normally formed by each conidiospore. In *Cystopus*, as we have seen, the zoosporangium gives rise on germination to a number of zoospores, which are not only actively motile but capable of affecting a separate infection of the host tissue. It follows that the structure producing these zoospores must be regarded as a zoosporangium, comparable with that of *Pythium.*

From this we may conclude that the typical conidiospore is equivalent to a zoosporangium in which the contents do not divide into separate zoospores but germinate by a germ tube. In *Cystopus* we see how one stage in the process of conidiospore formation may have been evolved by abstricting these zoosporangia in chains.

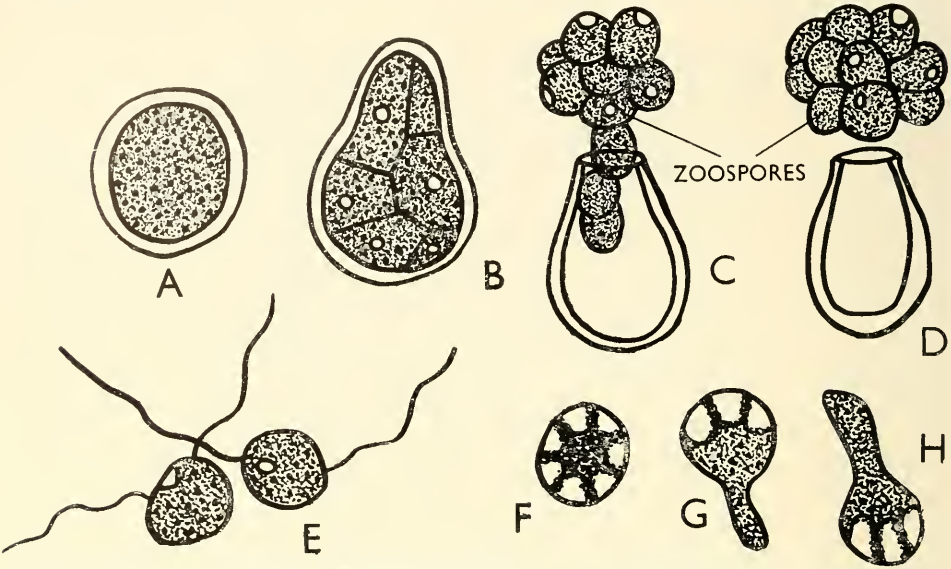

Fig. 229.—*Cystopus candidus.* Asexual reproduction. A, Zoosporangium. B, Septation of zoosporangium. C and D, Discharge of zoospores. E, Flagellated zoospores. F, G and H, Germination of zoospores. (*After de Bary.*)

Sexual Reproduction

The sex organs are developed in the intercellular spaces of the host tissue and very often in the deeper layers of the stem. They consist of **oogonia** and **antheridia.** The oogonium is globose and is developed from a terminal, or occasionally from an intercalary swelling of a hypha. The mature oogonium may contain as many as a hundred nuclei, together with a quantity of food material. It is finally cut off by a septum from the rest of the hypha. The antheridium is club-shaped and is developed in close association with the oogonium. It is also multinucleate, containing some twelve nuclei, and it is also separated from the supporting hypha by a septum (Fig. 230). At this stage the nuclei in both the oogonium and antheridium simultaneously undergo one nuclear division.

At about the time when the antheridium comes into contact with the oogonium the protoplasm of the latter undergoes differentiation, leaving a zone of rather translucent **periplasm** surrounding the denser **oosphere,** which contains most of the nuclei. At the point of contact of the antheridium and the oogonium the antheridial wall becomes very thin and the oogonium pushes its way in, forming a slight protuberance, which is called the **receptive spot.** It appears to be functionless, for shortly afterwards there develops from the antheridium a **fertilization tube,** which penetrates the receptive spot and enters the oosphere. All the nuclei in the antheridium and the oosphere now undergo a second nuclear division, while the nuclei in the periplasm disorganize. A single female nucleus passes to the centre of the oosphere and remains there, while the others pass to the periphery and finally abort. A single nucleus from the antheridium, together with a small amount of cytoplasm, passes in through the fertilization tube and the male and female nuclei come into contact and fuse. The fertilization tube collapses and is withdrawn from the oosphere, leaving a large vacuole. The wall of the **oospore,** thus formed, is now laid down. It is a thick, two-layered structure consisting of a thin **endospore** and a thick, often almost spiny, **exospore** (Fig. 231).

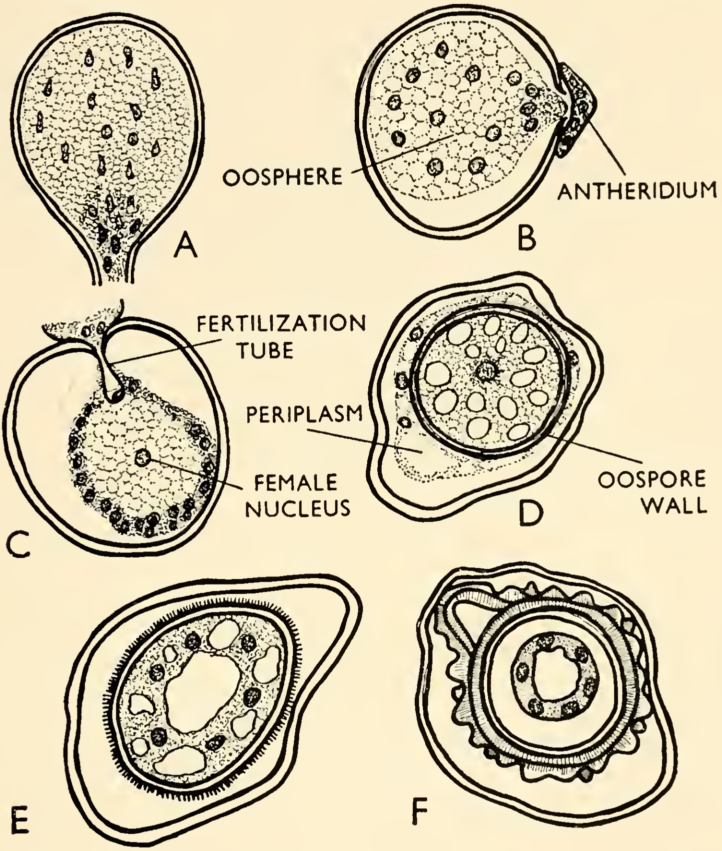

Fig. 230.—*Cystopus candidus.* Sexual reproduction. A, Mature oogonium. B, Formation of receptive spot in connection with antheridium. C, Development of fertilization tube. D, Post-fertilization stage, with oospore wall appearing and single fusion nucleus. E, Later stage in oospore formation with multiple nuclei. F, Mature thick-walled oospore, including remains of fertilization tube. (*After Wager.*)

Inside the oospore the zygote nucleus begins to divide, resulting in the formation of about thirty nuclei, after which activity temporarily ceases, and the oospore may remain for a long time in this condition. Later when germination occurs the wall splits and about a hundred **zoospores** are liberated. It is obvious, therefore, that prior to germination further nuclear divisions must take place, and though it has never been conclusively demonstrated, it appears likely that each of the thirty nuclei found in the oospore after fusion undergoes two divisions, which involve a meiosis, so that the nuclei of the zoospores are monoploid.

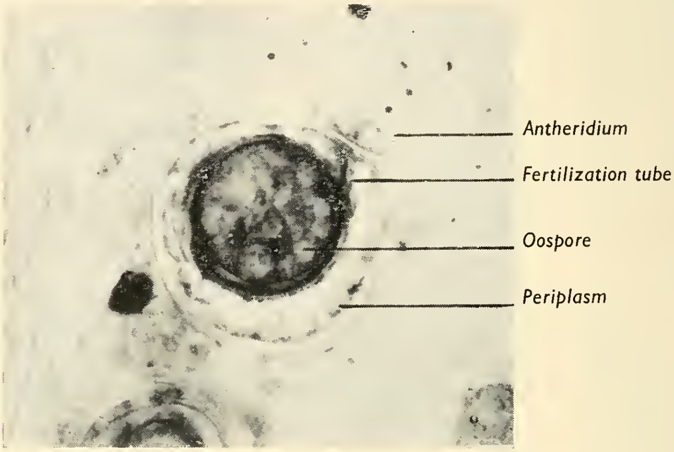

Fig. 231.—*Cystopus candidus.* Mature oospore in host tissue.

The life-history of *Cystopus candidus* may be represented by the following diagram (Fig. 232):—

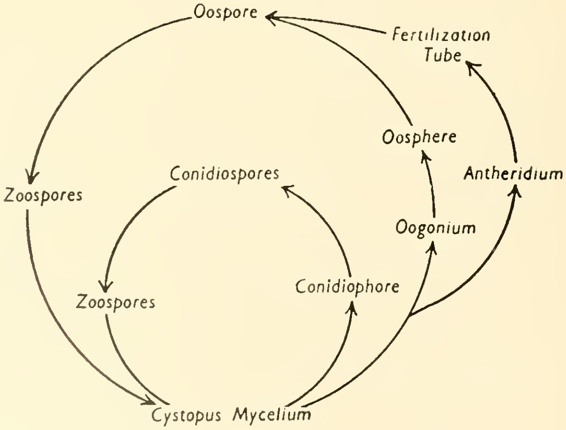

Fig. 232.—Life-cycle of *Cystopus candidus.*

The Fungus is not a serious disease of cultivated crucifers, for though it frequently attacks them, it is rarely that the host plant is seriously affected. The oospore can apparently retain its vitality for as much as four years. The infection of the host takes place only through the cotyledons of the seedling or through such delicate tissue as the flower buds. The parasite cannot penetrate the mature epidermis, consequently an epidemic spread of the disease among crucifers is not very likely.

Despite the fact that *Cystopus* was the first name given to this fungus, and therefore undoubtedly the correct one, American workers have for many years used the name *Albugo*. The confusion is increased by the fact that the genus is now included in a separate family of the Peronosporales under the name Albuginaceae, in which the type genus is, according to European workers, *Cystopus*.

Mucorales

The Mucorales are Phycomycetes in which the sex organs are relatively simple, and in which sexual reproduction may only occur at very infrequent intervals. When it takes place it consists of the fusion of two non-motile gametes. In most forms, including *Mucor*, these are morphologically identical, but in some other types they differ in size. Asexual reproduction is by means of aerially distributed spores, which may either be enclosed in a sporangium or may be abstricted in chains from conidiophores.

We shall consider only one example of this order, *Mucor*.

Mucor mucedo (The Common Bread Mould or Pin Mould)

This Fungus lives exclusively as a saprophyte and is frequently found producing a whitish-grey down on bread, cheese, jam, and other food material. It is also very widely distributed in the humus of the soil. It may be cultivated by keeping damp horse-dung or bread under a bell-jar for a few days (Fig. 233).

The **mycelium** of *Mucor* consists of long, slender **hyphae**, generally white or colourless, which ramify over the surface of the food material and send down absorptive hyphae into it, for it is by this means that the essential nourishment is taken into the mycelium. These hyphae are coenocytic, though cross walls may occur at intervals in old hyphae.*

The Fungus grows very rapidly, covering the substance on which it is feeding. Concurrently with growth there is abundant provision for reproduction. Normally this is effected asexually by means of spores, though sexual reproduction occurs very occasionally and under special conditions, which we shall discuss later.

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* In *Rhizopus nigricans* (*Mucor stolonifer*), a very common species, the mycelium gives rise to arched, aerial stolons, which do not branch but grow rapidly in all directions. At intervals these stolons produce tufts of brown rhizoids which penetrate the substratum, and opposite each tuft of rhizoids there arise one or more pairs of upright sporangiophores.

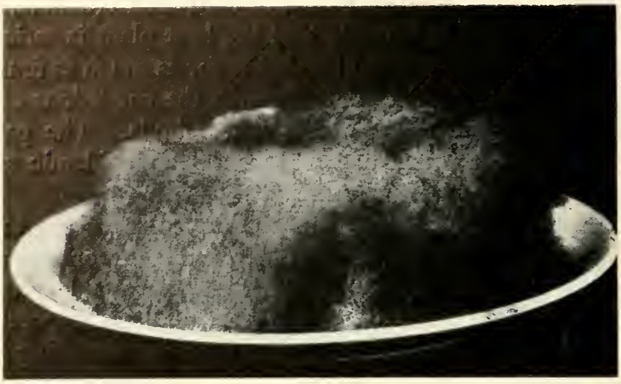

FIG. 233.—*Mucor sp.* growing on a piece of damp bread showing black sporangia.

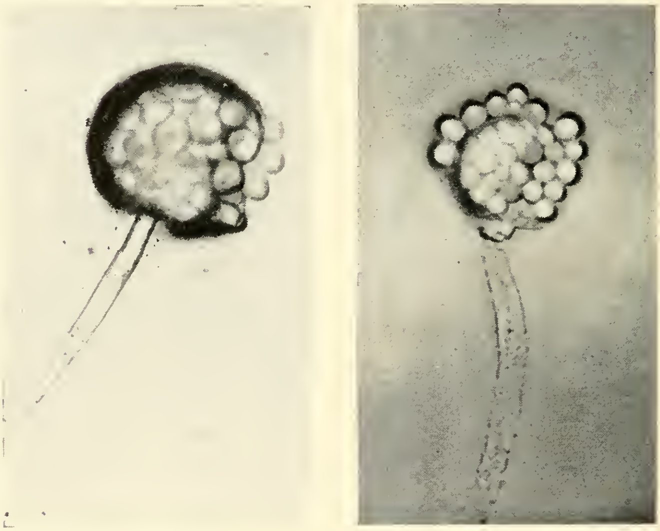

FIG. 234.—*Mucor mucedo.* Two stages in the dehiscence of sporangium.

ASEXUAL REPRODUCTION

Within a few days of the appearance of the mycelium asexual reproduction begins. Vertical hyphae (**sporangiophores**) grow out from the mycelium, which are destined to produce terminal **sporangia.** The sporangium is formed by the enlargement of the apex of the hypha into a spherical vesicle containing many nuclei. The protoplasm of the sporangium is divided by cleavage planes into uninucleate masses, from each of which an ellipsoidal spore is formed. By a similar cleavage plane a dome-shaped septum is formed in the basal part of the sporangium, called the **columella,** which separates the body of the sporangium from the sporangiophore (Fig. 235). The wall of the sporangium hardens and becomes brittle, and the entire sporangium darkens in colour until it is almost black when mature. The wall is covered with a deposit of small crystals of calcium oxalate. Not all species of *Mucor* produce terminal sporangia. In some they may be developed on branched hyphae or in clusters. It is on such characters as these that the species are chiefly separated.

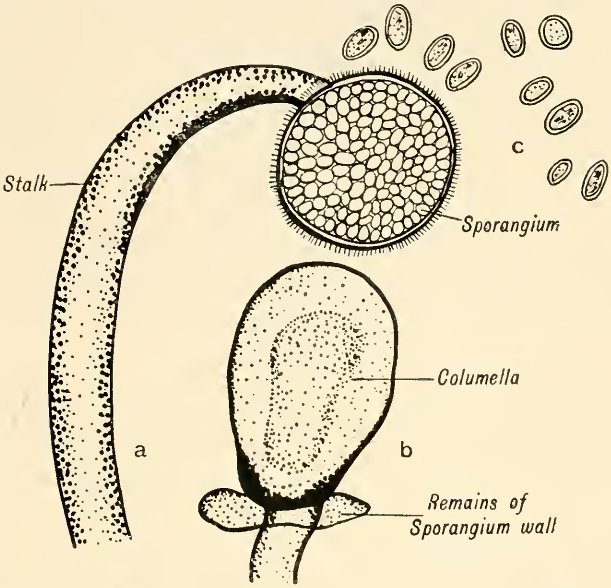

Fig. 235.—*Mucor mucedo.* Asexual reproduction. A, Mature sporangium before dehiscence. B, After dehiscence. C, Spores.

When mature the sporangium wall is surrounded by a drop of water, secreted by the sporangiophore, and breaks round the base, leaving a ragged collar attached to the sporangiophore. The spores are not immediately shed but remain clinging together in a wet mass, and the means of their dispersal is uncertain. It has been claimed that insects are the chief agents, but it seems probable that eventually, when the whole mycelium has died and dried up, that some spores at least are scattered in the air. Their wide dispersal, especially in the soil, is otherwise difficult to understand (Fig. 234).

Spores germinate immediately on reaching a suitable substratum and produce a hypha from which a new mycelium develops.

Sexual Reproduction

It is well known that zygospores are only rarely found in cultures of *Mucor*, but for long the reason for this was not understood. It was shown by Blakeslee in 1904 that the mycelium of the Fungus is unisexual and not capable of producing both male and female gametes. Sexual reproduction, therefore, can only occur when different mycelia intermix. Two distinct types exist, which are called " plus " and " minus " respectively. Zygospores can only be formed when mycelia of both types meet. There is no morphological distinction between the mycelia, though obviously there must be a physiological one. Such a condition, where the thalli are morphologically alike but physiologically different, is termed **heterothallism.** It is widespread in the Fungi, and many species are found to exhibit this phenomenon.

When the hyphae of the two strains come into contact, short lateral branches, called **progametangia,** are developed, which adhere together by their tips (Fig. 236). They swell and a transverse septum appears in each, cutting off a terminal cell or **gametangium.** The remainder of the progametangium is known as the **suspensor.** These gametangia are multinucleate, and when mature the wall between them breaks down and a single **fusion cell** is formed. The wall of the fusion cell becomes thickened and dark coloured, and develops a rough warty surface. This cell is now termed the **zygospore** (Fig. 237). The thick wall forms the **exospore,** while within it is a thin membrane called the **endospore.** The suspensors wither and the zygospore is set free (Fig. 238).

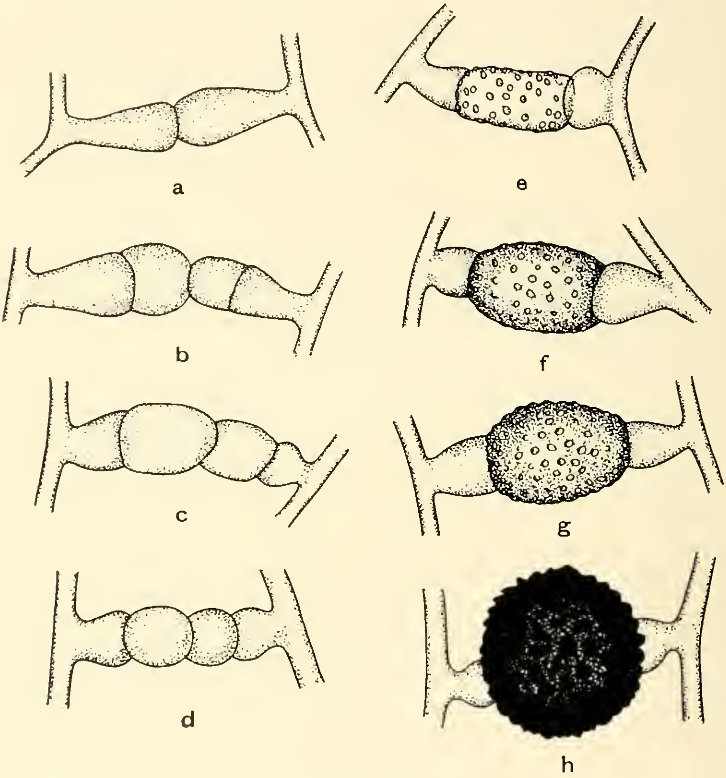

FIG. 236.—*Mucor mucedo.* Sexual reproduction. A, Progametangia adhering. B, C and D, Differentiation of gametangia and suspensors. E, Formation of fusion cell. F and G, Development of zygospore. H, Mature zygospore.

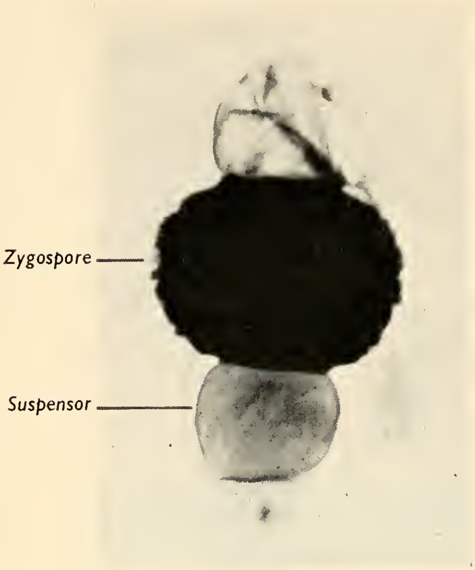

FIG. 237.—*Rhizopus nigricans.* Isolated zygospore with attached suspensors.

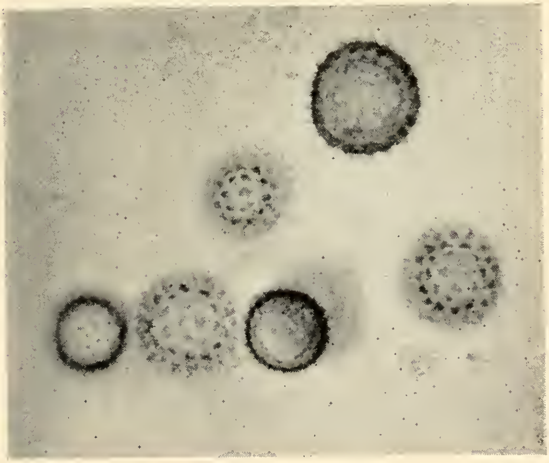

FIG. 238.—*Mucor hiemalis.* Detached zygospores with spiny exospores.

Various interpretations of the nuclear behaviour inside the zygospore have been suggested, but owing to the very small size of the nuclei there is no agreement between the views expressed. It may be that there is general pairing of the nuclei, so that a number of diploid nuclei are produced, or, as seems more likely, that only one nucleus from each gametangium actually fuses.

The zygospore retains its vitality for a considerable time and undoubtedly will resist unfavourable conditions. Since, however, zygospore formation is rare, it must not be regarded as the chief method of tiding the Fungus over bad conditions, for the asexual spores appear perfectly capable of doing this. When germination of the zygospore occurs the wall splits open and a single hypha grows out which terminates in a sporangium. Considerable importance is attached by some to this hypha, which is called a **promycelial hypha,** and to the sporangium which it produces. However, the structure of the sporangium differs in no way from the typical sporangium produced asexually, and the spores produced in it give rise to fresh mycelia in due course.

No definite information is available as to the position of meiosis, though various workers have studied the problem. According to some the zygote nucleus divides into four prior to germination, a condition analogous with what occurs in *Spirogyra*. Many suggest that reduction division occurs in the sporangium borne on the promycelial hypha. It is on account of this latter view that the hypha produced by the zygospore assumes special importance for, if reduction division occurs in the sporangium it produces, this hypha must be diploid, in contrast to the rest of the mycelium. Moreover, the sporangium formed on it must also be regarded as distinct, since, unlike asexual sporangia, it is the seat of meiosis. In the light of our present knowledge, however, we cannot say where meiosis occurs, nor are we sure that there is actually any nuclear fusion in the zygospore, though it is reasonable to assume that there is. If so, then at some subsequent stage there must be a meiosis to bring back the nuclei to a monoploid state.

The life-cycle may be graphically represented by the scheme shown in Fig. 239.

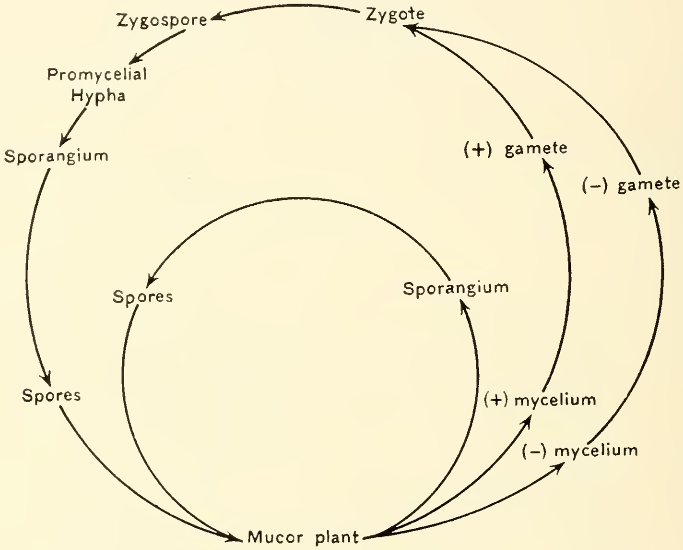

Fig. 239.—Life-cycle of *Mucor*.

As in the previous genera we can trace the gradual evolution of a conidiospore from the sporangium of *Mucor*. The conidiospore condition seems to have been reached by the gradual reduction in the number of spores produced in a sporangium until there is only one, when the body may be truly regarded as a conidiospore, since it germinates by a germ tube.

HETEROTHALLISM

The phenomenon of heterothallism is so important in the Fungi that we must say something more about it. Though the process was first discovered in the Mucorales by Blakeslee in 1904, it has now been shown to occur in many families of Fungi. In many species there is nothing in the structure of the mycelia to distinguish them from one another, but where they meet a line of zygospores is formed (Fig. 240). In such cases it is customary to speak of one strain as plus (+) and the other as minus (−).

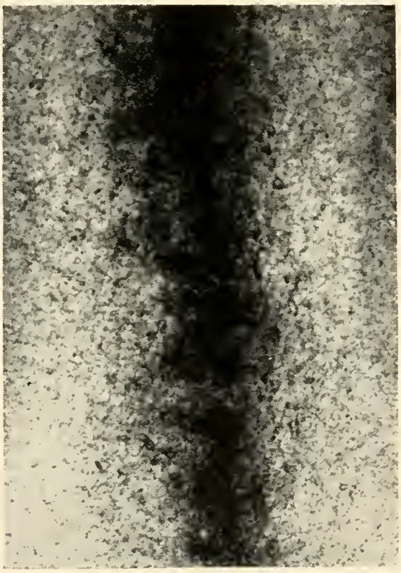

FIG. 240.—*Mucor hiemalis*. Culture of (+) and (−) strains showing formation of zygospores at line of meeting.

In a few species of *Mucor* it has been found that zygospores are produced by the interaction of hyphae in a mycelium produced from one spore, and such species are said to be **homothallic.** In some instances **imperfect hybridization** may occur between opposite strains of different heterothallic species and between both (+) and (−) strains of heterothallic species on the one hand and homothallic species on the other. In such cases only the early stages are gone through and the mature zygospore is never produced.

In certain other genera the gametangia of homothallic species are either not quite alike, or they may even differ markedly from one another. Such a species is said to be a **heterogamic homothallic** one. One such example is *Absidia spinosa* in which the gametangia are of different sizes. Here the larger is regarded as equivalent to the female and the smaller to the male gamete. It has been found possible to produce a hybrid between *Absidia spinosa* and *Mucor hiemalis*, which has identical gametangia, that is, it is **homogamic** but **heterothallic**. As a result of such a cross it has been discovered that the (–) strain of *Mucor hiemalis* united with the larger gametangium of *Absidia spinosa*, while the (+) strain of *M. hiemalis* united with the smaller gametangium. It is therefore concluded that the (+) strain of a heterothallic homogamic species is the female strain, while the (–) strain is male. It may be mentioned that, as a result of biochemical tests, these conclusions of Blakeslee have been substantiated (see Volume III).

CHAPTER VII

THE FUNGI : ASCOMYCETES AND BASIDIOMYCETES

ASCOMYCETES

THE Ascomycetes are Fungi whose fruiting bodies are either composed of interwoven filaments or of a pseudoparenchyma consisting of a compact tissue of filaments. They may be sac-like **perithecia,** either completely closed or flask-shaped and opening by an ostiole, or even open cups—**apothecia.** Within the fruiting bodies sac-shaped **asci** are developed, in which eight (sometimes four or sixteen) **ascospores** are formed. The spores are forcibly ejected from the asci and form new mycelia. The asci may originate from the fusion of nuclei, derived from an oogonium and **antheridium,** but in many instances there has been a great degeneration of the sex organs, and sexual conjugation consists simply in the fusion of two vegetative nuclei. In the Ascomycetes the oogonium is frequently called the **ascogonium** from the fact that it produces asci. Asexual reproduction is by **conidiospores.** Many species are of great economic importance as the cause of serious plant diseases.

The Ascomycetes are divided into a number of orders of which we shall consider examples of the following :—

1. **Plectascales** (*e.g.*, *Aspergillus*).
2. **Erysiphales** (*e.g.*, *Sphaerotheca*, *Erysiphe*).
3. **Pezizales** (*e.g.*, *Pyronema*, *Peziza*).
4. **Helvellales** (*e.g.*, *Helvella*).
5. **Phacidiales** (*e.g.*, *Rhytisma*).
6. **Saccharomycetales** (*e.g.*, *Saccharomyces*).
7. **Hypocreales** (*e.g.*, *Claviceps*).
8. **Sphaeriales** (*e.g.*, *Hypoxylon*).
9. **Laboulbeniales** (*e.g.*, *Stigmatomyces*).

Plectascales

The Plectascales are Ascomycetes in which the product of the fertilization of the ascogonium is frequently only a single ascus. In some of the higher members, where more than a single ascus is produced, the asci are not arranged in any system, but are scattered irregularly in a special closed body termed the **perithecium.**

We shall consider one example of this order, *Aspergillus*.

Aspergillus (Eurotium) herbariorum

This Fungus is a saprophyte on fatty substances and forms one of the most frequent contaminants of food. Some species are parasitic on man and animals, but the majority live as saprophytes. The mycelium consists of filaments of multinucleate cells, and ramifies over the surface of the substratum on which it lives, sending up vertical hyphae which bear the asexual reproductive organs. The name *Eurotium* was originally applied to the sexual stage, while the name *Aspergillus* was used for the asexual. This was due to the fact that until comparatively recently the two stages were regarded as those of distinct Fungi, owing to the fact that either stage could apparently continue indefinitely without the appearance of the alternative stage. This tendency among Fungi for the asexual stage to continue generation after generation without the intervention of a sexual stage we have already met with in *Mucor*. It is equally true of many of the Ascomycetes, in fact there exists a large group of Fungi, termed the **Fungi Imperfecti,** which includes many important plant pathogens, and comprises Fungi in which only the asexual stage is known (see Volume IV).

Asexual Reproduction

The asexual reproductive bodies are borne on **conidiophores** (Fig. 241) These arise as vertical hyphae which grow out from the mycelium. They are thick and are not divided by septa. The tips of these conidiophores

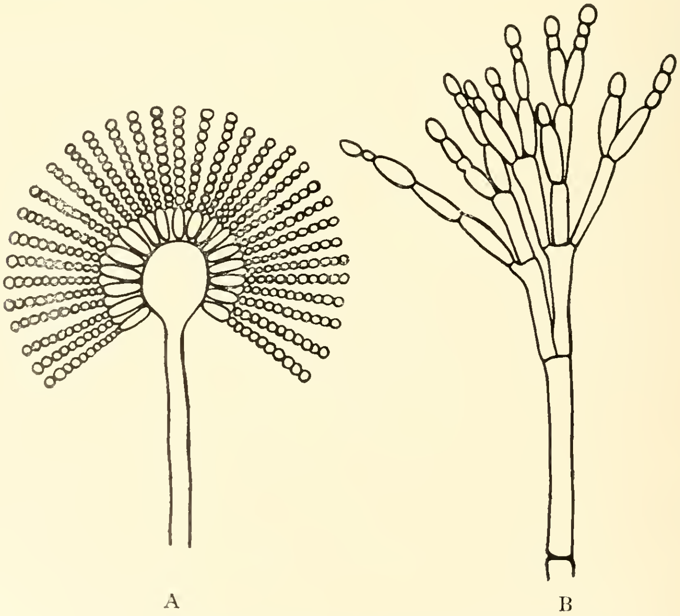

Fig. 241.—Comparison of conidiophores. A, *Aspergillus niger*. B, *Penicillium camembertii*.

become swollen and bud out numerous small processes, the **sterigmata,** from each of which **conidiospores** are produced in chains in acropetal succession. The spores are distributed by air currents, and on coming to rest on a suitable substratum each germinates to produce a hypha from which a fresh mycelium develops.

Sexual Reproduction

The **archicarp** or fruit primordium consists of three parts: a multicellular stalk, an elongated unicellular ascogonium, and a unicellular **trichogyne** (Fig. 242). The antheridium arises from the same initial hypha as the ascogonium, or from an adjacent one. It is unicellular and multinucleate. Fusion takes place between the antheridium and the trichogyne, which become twisted around one another during the process. It has not been proved, however, that the antheridium is ever functional in fertilization. In some species the antheridium may be absent, but this does not prevent the further development of the ascogonium. In either case the ascogonium becomes divided into a number of binucleate cells, from each of which a septate **ascogenous hypha** is given off. From the terminal cell of each hypha or from the cell below, termed the **penultimate cell,** an **ascus** is formed by elongation. In this cell the two nuclei fuse together.

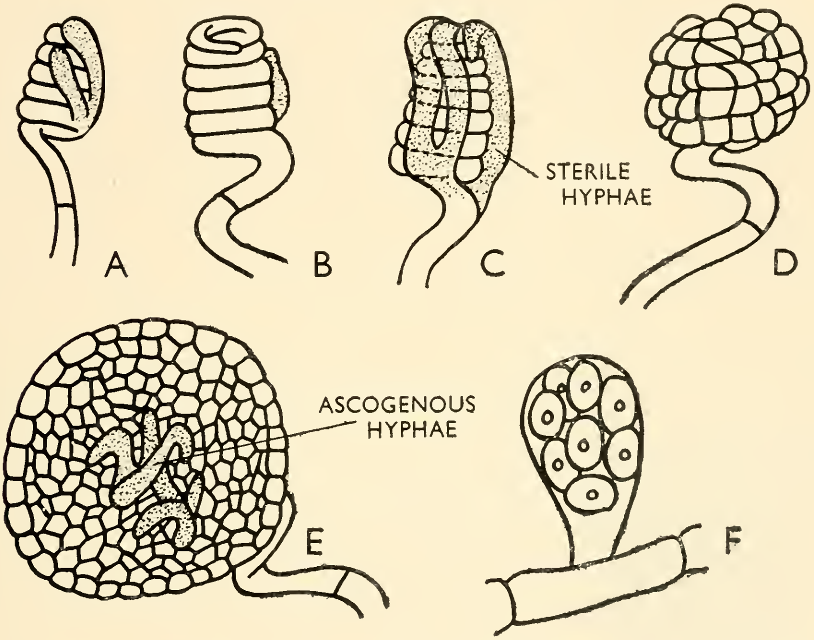

Fig. 242.—*Aspergillus herbariorum.* A to D, Stages in the development of the perithecium around the sex organs. E, Section through perithecium showing ascogenous hyphae. F, A single ascus containing ascospores. (*After de Bary.*)

Shortly after the development of the sex organs, hyphae begin to grow up around them and the whole structure becomes enclosed in a two-layered envelope, the **perithecium,** the inner layer of which forms a nutritive tissue, while the outer serves for protection. This latter tissue secretes a bright yellow substance which makes the sexual reproductive bodies easily recognizable.

After the fusion of nuclei within the ascus the zygote nucleus so formed divides meiotically into four, and this is followed by a further mitotic division. Around each of these eight nuclei a wall is laid down forming an **ascospore.** These spores have a sculptured epispore wall and are rounded in shape. They are liberated upon the decay of the perithecium surrounding the reproductive organs. They germinate to produce fresh mycelium (Fig. 243).

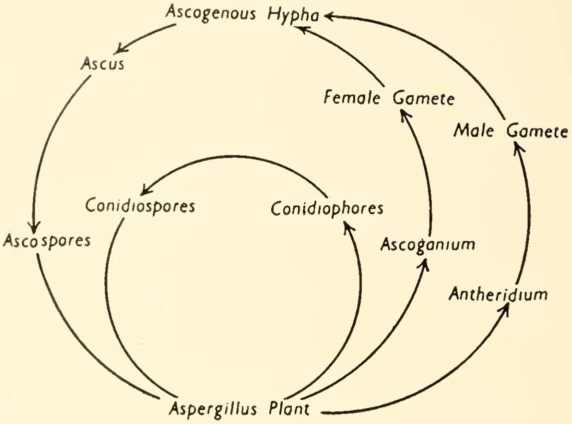

FIG. 243.—Life-cycle of *Aspergillus herbariorum.*

Closely allied to *Aspergillus* is the genus *Penicillium,* which is used, associated with other Fungi, in the " ripening " of cheese. It differs chiefly from *Aspergillus* in the form of the conidiophore (Fig. 244). The conidiophores are narrow and branched and not swollen at their tips, while the conidiospores are abstricted in more or less parallel chains. The sexual reproduction is similar to that of *Aspergillus.* The well-known antibiotic substance Penicillin is a product of *Penicillium notatum.*

FIG. 244.—*Penicillium sp.* Branched conidiophore with conidiospores abstricted in chains.

Erysiphales

The Erysiphales are Ascomycetes which are characterized by an abundant mycelium, which is often dark coloured. The sex organs are enclosed within a tissue termed the perithecium, which is without an ostiole. The asci are formed together in a group from a regular layer in the base of the perithecium.

Many of them cause the White or Powdery Mildews or Blights on flowering plants, where they live as parasites on the leaves. They are almost cosmopolitan in distribution, but have been most commonly found in Europe and North America.

We shall consider two examples of this order, *Sphaerotheca humuli* and *Erysiphe polygoni* because of the marked difference in the methods of sexual reproduction.

Sphaerotheca humuli (The Hop Mildew)

This Fungus is the cause of Hop Mildew or Mould and is one of the most serious diseases of the Hop. It chiefly affects the leaves and the young strobili, rendering the latter useless. The intensity of the disease varies from season to season and is best controlled by dusting the hop bines with finely powdered sulphur.

The life-cycle begins with the germination of either the asexual conidiospore or the sexual ascospore upon the surface of the host plant. A series of hyphae are formed which spread over the surface of the leaf, producing a white web-like coating with uninucleate cells. From these hyphae slender branches penetrate the cuticle and grow down into the epidermal cells, forming ramifying branches within the cells by which food is absorbed. These special cells are termed **haustoria,** and are the only part of the Fungus which enters into the host plant. Penetration by the haustoria is secured in a peculiar manner. The mycelial hyphae send out short branches which apply themselves very closely to the epidermis of the host and spread out into an adhesive disc called an **appressorium.** From the centre of this disc appears a new and extremely fine outgrowth which pushes through the cuticle like a needle-point. On entering the cell this outgrowth enlarges into a normal-sized hypha and branches freely.

ASEXUAL REPRODUCTION

During the summer months reproduction is asexual by means of **conidiospores.** The **conidiophores** are short, upright, unbranched hyphae which abstrict from their upper ends single chains of large oval conidiospores (Fig. 245).

SEXUAL REPRODUCTION

Sexual reproduction in *Sphaerotheca humuli* occurs in the late summer by the formation of **perithecia,** which are spherical structures 0·05 to 0·3 mm. in diameter and furnished with simple **appendages.** The perithecium is formed by a mass of hyphae which aggregate into a tiny ball. It is white at first, but as it matures it turns clear yellow, and finally brown.

The sexual organs arise as lateral branches from the mycelium (Fig. 246). The **ascogonium** arises from a cell which divides to form a stalk cell and an oogonial cell, the latter being uninucleate. The **antheridium** is smaller and is also borne on a narrow stalk cell. It also contains a single nucleus. Antheridium and ascogonium stand side by side in close apposition. The wall between the two sex organs breaks down, and the male nucleus enters the ascogonium and unites with the female nucleus. Nuclear division follows and the zygote cell divides into a row of cells, the penultimate cell of which contains two nuclei. This row of cells is equivalent to an **ascogenous hypha.** From the penultimate cell the **ascus** is produced. While this is going on, hyphae form around the developing sex organs, producing the wall of the perithecium. The two nuclei in each ascus then fuse, and immediately the zygote nucleus divides into four, during which reduction occurs. This is followed by a further mitotic division which, according to some workers, is also reductional. Thus eight nuclei are formed in each ascus and around them walls are formed producing the eight **ascospores.**

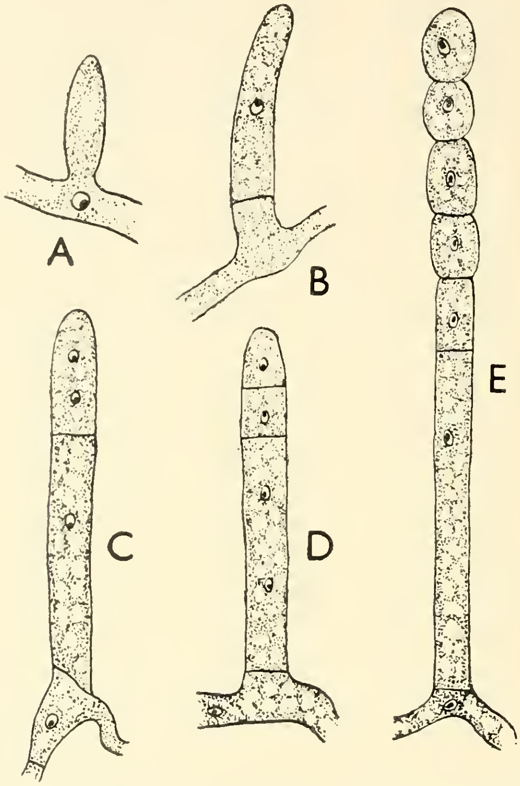

FIG. 245.—*Sphaerotheca humuli.* Asexual reproduction. A to D, Stages in the development of the conidiophore. E, Septation of conidiospores. (*After Foëx.*)

It will be seen from this account that there may be two fusions, one in the ascogonium itself and a second in the ascogenous hypha, and hence, to bring the chromosome number back to the monoploid, two reduction divisions are necessary. According to many workers a nuclear fusion does not occur in the ascogonium, but there is merely an association of nuclei, and they consider that the only true fusion occurs in the ascogenous hypha. If this is the case there is only one reduction division, namely the first division of the nucleus in the ascus.

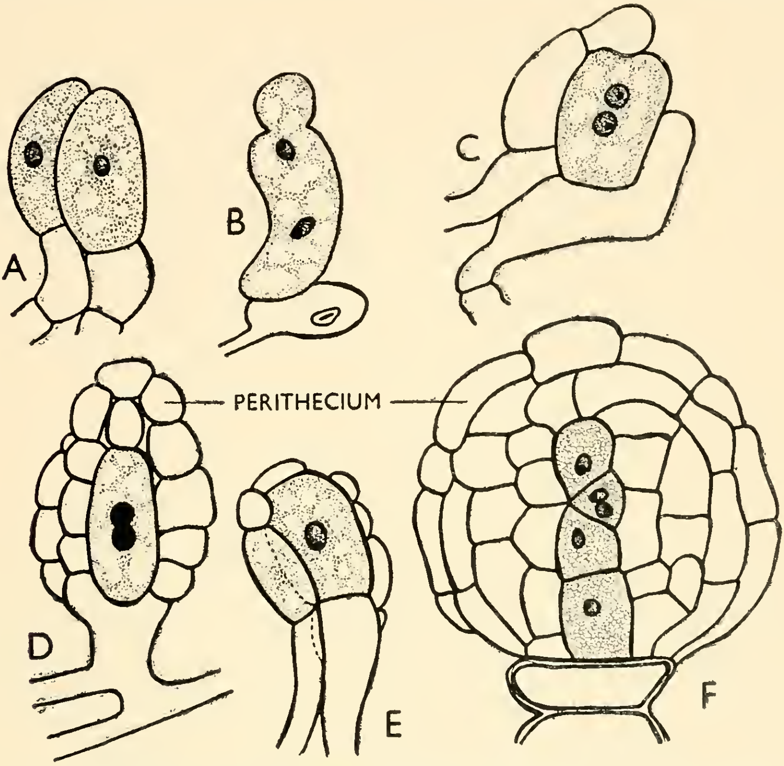

Fig. 246.—*Sphaerotheca humuli.* Sexual reproduction. A, Associated ascogonium and antheridium. B, Ascogonium with male and female nuclei, the antheridium lies behind the ascogonium. C, Male and female nuclei in ascogonium. D and E, Ascogonium with fusion nucleus. F, Formation of perithecium and division of ascogonium into a row of four cells, the penultimate cell of which is binucleate. (*After Harper.*)

During development the wall of the perithecium becomes differentiated into inner and outer layers, which can be easily distinguished. The inner layer is made up of thin-walled cells, rich in protoplasm. It forms a packing round the developing asci and supplies them with food. The function of the outer layer is for protection. Its cells have scanty contents and their walls undergo a change analogous to lignification.

From special cells of this layer the characteristic filamentous appendages are differentiated. These appendages consist of long, single-celled outgrowths which show various degrees of complexity in different genera. Their shapes are quite characteristic and are chiefly used as a basis of the separation of the genera.

The life-cycle of *Sphaerotheca humuli* is represented in the following diagram (Fig. 247).

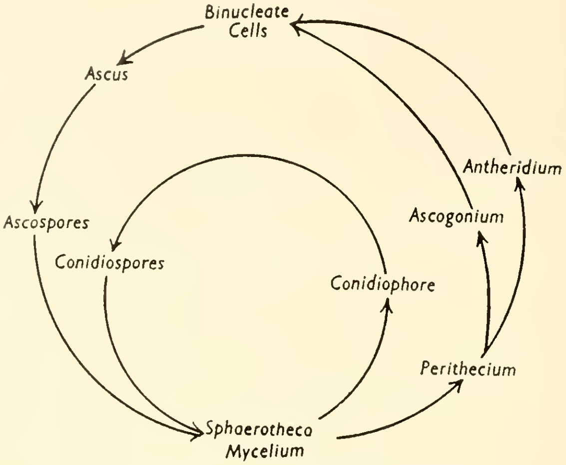

Fig. 247.—Life-cycle of *Sphaerotheca humuli.*

In the classification of the Powdery Mildews we have a clear and simple example of the principles of plant classification, and it may be worth while to mention it briefly here. The genera fall naturally into two groups ; firstly those with only one ascus in each perithecium, and secondly those in which more than one ascus is produced. In the former section there are two genera : *Sphaerotheca*, in which the appendages are long and hyphal-like, and *Podosphaera*, in which the ends of the appendages are repeatedly and dichotomously branched. In the second group are four common genera : *Erysiphe*, in which the appendages are like those of *Sphaerotheca* ; *Microsphaera*, in which they closely resemble *Podosphaera* ; *Uncinula*, in which the tips of the appendages curl inwards ; and, finally, *Phyllactinia*, in which they are straight and stiff with a swelling at the base. The following diagram brings out these points clearly (Fig. 248).

Erysiphe polygoni (The Pea Mildew)

This species causes a Mildew of Peas and also of Swedes and Turnips. In the former case it may attack the pods as well as the leaves. Swedes and Turnips are often attacked in a dry summer to such an extent that the leaves are turned completely white by the mycelium.

The Fungus spreads over the surface of the host plant, sending down fine **haustoria** into the epidermal cells where they spread out forming absorptive organs. During the summer months reproduction is by means of conidiophores which abstrict conidiospores in chains (Fig. 249). These are entirely similar to those in *Sphaerotheca* both in their development and

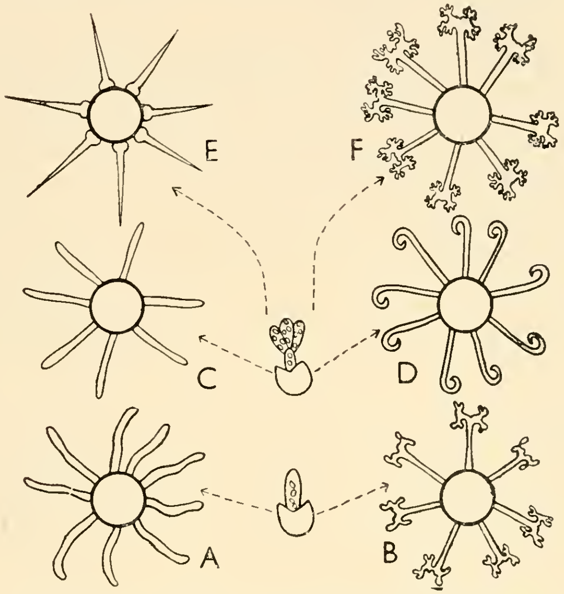

FIG. 248.—Comparison of the perithecia in Erysiphaceae. A, *Sphaerotheca*. B, *Podosphaera*. C, *Erysiphe*. D, *Uncinula*. E, *Phyllactinia*. F, *Microsphaera*. A and B are uniascoid, C to F are multiascoid. (*After Heald.*)

form, and we need not consider them here. In fact it is only in the method of formation of the sexual reproductive organs that this species displays an interesting and important difference.

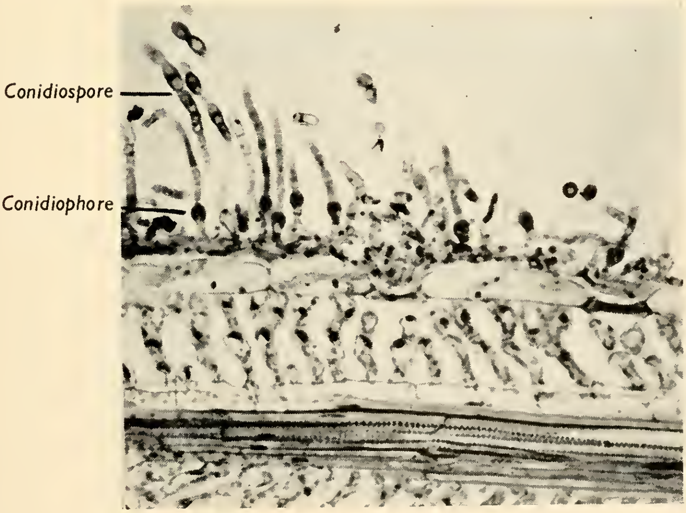

FIG. 249.—*Erysiphe polygoni*. Formation of conidiophores on surface of infected leaf. Haustoria may be seen in the epidermal cells.

SEXUAL REPRODUCTION

Initially there is a conjugation between short branches of two adjacent hyphae, with the result that a **fusion cell** is formed (Fig. 250). There is no evidence that any nuclear fusion occurs, though the nucleus of one hypha passes into the other. This stage is followed by formation of additional cells, which are budded off the fusion cell, or **central cell.** The cross walls of these cells are not closed, and the whole structure forms a coenocyte or **maze,** as it is sometimes called. Meanwhile, additional tissue grows up surrounding this maze and forming the inner and possibly the outer wall of the perithecium.

After a while the cells of the maze break down to form a cavity in the centre of the perithecium, while by the formation of additional septa the cells of the perithecium, which were originally multinucleate, become progressively uninucleate.

From near the base of the perithecium there then grow up into the cavity, several cells each of which is binucleate. Their nuclei fuse, and in this way a number of asci are produced. The fusion nuclei divide meiotically, followed by a second and third division to form the eight nuclei of the ascospores, around each of which the spore wall is ultimately formed.

When mature the whole perithecium is blown away by the wind, and may become attached to a fresh leaf by the appendages (Fig. 251). Here the wall of the perithecium breaks down and the asci burst, liberating the ascospores, which germinate, forming fresh hyphae. It is generally found that the ascospores are not formed until the spring, since the perithecium over-winters on the ground among dead grass, development stopping in the autumn at the formation of the asci (Fig. 252).

BIOLOGIC RACES

Recent work has shown that in *Erysiphe graminis* there are several **biologic races,** that is to say that different strains exist, which are morphologically indistinguishable but among which it can be shown that the strain which attacks one species of grass will not infect any other grass. Similarly, cultivated cereals each have their own particular strain. A point of some interest is the existence of **bridging species** among the host plants of the biologic strains of *E. graminis*. Thus the strain which infects *Bromus racemosus* will not attack *B. commutatus* directly, but it will attack *B. hordeaceus*, and an infection from the latter species will attack *B. commutatus*. No explanation is forthcoming as to what advantage the fungus derives from this very specialized restriction of possible host plants. We shall, however, meet with the same specialization in *Puccinia graminis*.

Similar biologic races occur in the types we have described. In *Sphaerotheca humuli* there is a biologic form which occurs on the cultivated strawberry, while in the United States there is a form which attacks roses. In *Erysiphe polygoni* the form which attacks Peas will not affect either Swedes or Turnips, while only the race on the latter plant is able to attack other species of *Brassica*, especially Kale. In England, however, this latter form rarely produces perithecia.

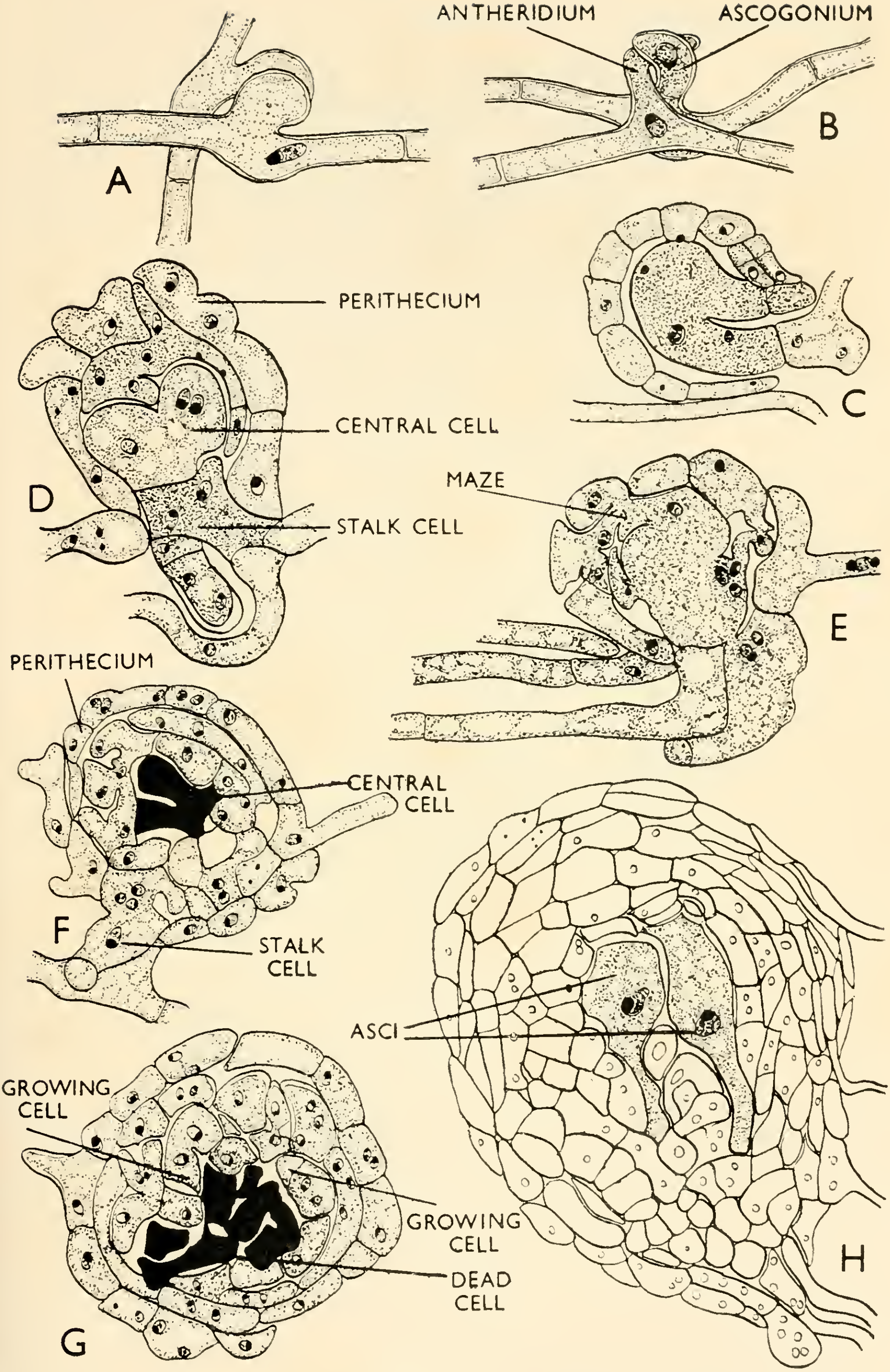

Fig. 250.—*Erysiphe polygoni.* Sexual reproduction. A, Two hyphae in contact pushing out branches. B, Branches twisting round one another. C, Young perithecium with fused sex organs. D, Perithecium with central cell and binucleated stalk cell. E, Perithecium with maze. F, Perithecium with degenerate central cell and multinucleate stalk cell. G, Perithecium with central group of dead cells and wall cells growing to form asci. H, Mature perithecium with two uninucleate asci in centre. (*After Allen.*)

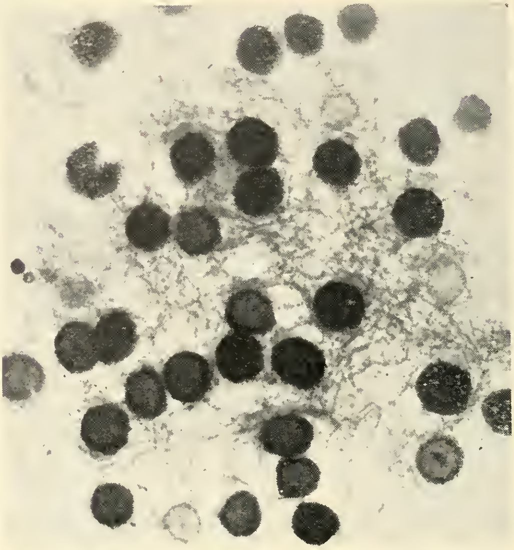

FIG. 251.—*Erysiphe graminis*. Perithecia with interlaced appendages.

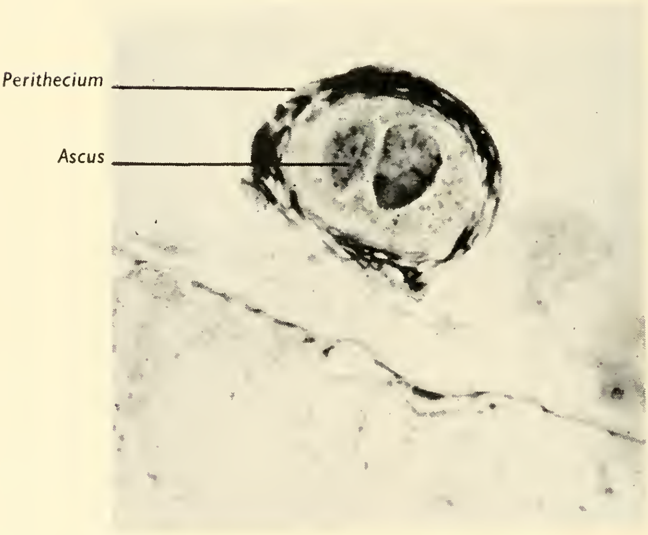

FIG. 252.—*Erysiphe cichoracearum*. Section through mature perithecium showing two asci.

Pezizales

The Pezizales are Ascomycetes in which the fruiting bodies have an outer covering which is either fleshy or leathery in texture. This definite external layer, or **peridium,** is closed at first, but subsequently is pushed open by the growth of sterile hairs or **paraphyses,** forming an open, cup-shaped or discoid **apothecium** lined with **asci.**

The group includes many common Fungi which occur on dead and decaying wood. Many of the fruiting bodies are brightly coloured and are conspicuous in woodlands during the autumn. We shall take as our examples *Pyronema confluens* and *Peziza vesiculosa.*

Pyronema confluens (P. omphalodes)

This little Ascomycete is sometimes found growing very abundantly in woods on burnt places, especially among half-charred masses of leaves, though it may also occur among damp well-decayed leaves even when there has been no fire (Fig. 253).

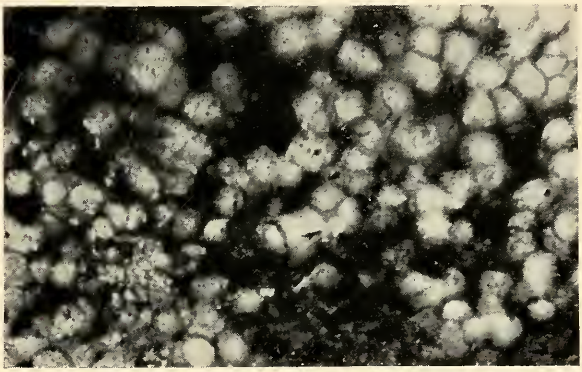

Fig. 253.—*Pyronema confluens.* Confluent apothecia on soil, about twice life size.

The mycelium is glistening white and resembles a frost-like tracery on the dark substratum on which it grows. It is on this mycelium that the sex organs are produced and only a few days are required for the development of these sex organs into mature fruiting bodies.

Pyronema confluens has gained a reputation out of all proportion to its importance either ecologically or morphologically, on account of the amount of work which has been done on its sexual reproduction, for it is the only known member of the Pezizales in which a complete sexual apparatus exists. It may therefore be regarded as the starting-point of a series of types showing a degeneration through which the true function of the sex organs is lost, and finally the organs themselves, till the sexual act is reduced to the fusion of two nuclei within a cell which is derived directly from the vegetative cells of the fruiting body, as we shall see in *Peziza.* As more and more of these simpler Pezizales are investigated more stages are supplied in this degeneration series, but so far *Pyronema confluens* stands alone in having the complete apparatus still present and functional. It is for this reason that we must consider the structure in some detail.

The Development of the Sex Organs

The cells of the mycelium are multinucleate and form a system of threads which ramify through the substratum. Among these hyphae branching is rare, but at certain points one or more forks appear from which branches grow upwards and form a small tuft. These filaments then branch dichotomously, and the terminal cells of paired branches become differentiated into a functional **antheridium** and a female organ, the oogonium or **ascogonium** (Fig. 254). Behind these are cut off one or two stalk cells, so that the antheridium forms a two- or three-celled branch, made up of uninucleate stalk cells and a multinucleate antheridium. The female branch consists similarly of one or two stalk cells, the swollen ascogonium and a **trichogyne** formed as a tubular process from the distal end of the ascogonium. Both the ascogonium and the trichogyne are multinucleate but unicellular.

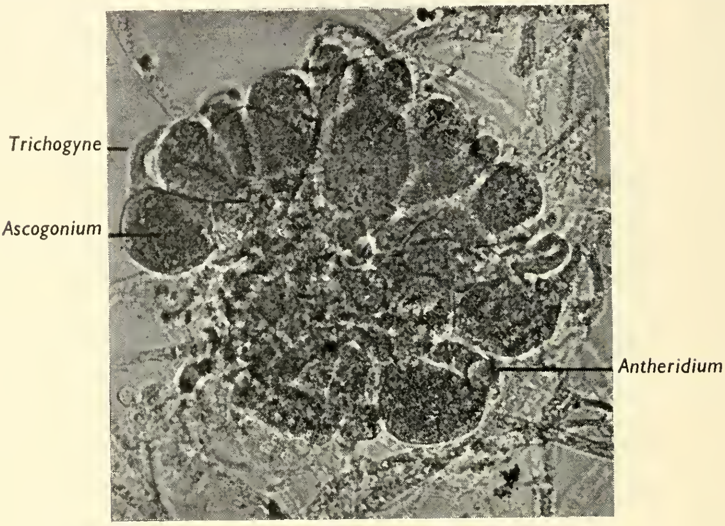

Fig. 254.—*Pyronema confluens.* Group of ascogonia with attached antheridia.

As growth continues the nuclei of both the ascogonium and the antheridium increase in size, while those of the trichogyne remain small and finally disorganize.

Fertilization

The trichogyne now comes into contact with the antheridium, and the wall between becomes dissolved. The male nuclei which have united into a cluster in the centre of the antheridium now migrate into the trichogyne, whose own nuclei have meanwhile disappeared. At the same time the wall separating the trichogyne from the ascogonium disorganizes and the nuclei of the ascogonium become grouped at its centre, while the surrounding cytoplasm becomes increasingly vacuolated. The male nuclei now pass down the trichogyne into the ascogonium and become associated with the female nuclei.

Whether these male and female nuclei actually fuse in pairs or whether they simply remain associated together is a matter of dispute. According to some workers there is definite nuclear fusion so that the resulting nuclei are diploid. Others consider that the male and female nuclei associate but do not fuse, so that they remain monoploid and subsequently divide in pairs (**conjugate division**).

The Ascogenous Hyphae

After a few hours changes have taken place in the fruiting body. In the first place the ascogonium has become enveloped in a tissue of vegetative hyphae which have originated from the lower cells of the original knot of tissue, thus forming the **peridium.** At the same time outgrowths have been formed from the wall of the ascogonium, and into each of these a pair of nuclei has made its way. These are the **ascogenous hyphae** (Fig. 255). They branch repeatedly, and by conjugate division each branch is supplied with a pair of nuclei or **dicaryon.** Septa now appear, cutting the hypha into a number of cells, each with one dicaryon in it. Finally the terminal cells bend over to form a hook like an inverted V, known as the **crozier,** and from the penultimate cell, which forms the apex of the hook, there grows out upwards a single elongated cell, the **ascus.**

The two nuclei of the dicaryon in the young ascus fuse. This fusion in the ascus is immediately followed by three nuclear divisions whereby eight nuclei are formed. It will be noted that there is no question about the nuclear fusion at this stage, hence it follows that if a nuclear fusion also did occur in the ascogonium then the fusion nucleus in the ascus must be tetraploid, seeing that it is formed as the result of two nuclear fusions. Alternatively, if there was only an association of male and female nuclei in the ascogonium and the sexual act was only consummated in the ascus, then the nucleus will be a typical diploid. Now, since obviously the nuclei of the ascospores must be monoploid, as they give rise to a monoploid mycelium, it follows that the normal procedure of meiosis will not provide the mechanism for reducing the chromosome complement of a tetraploid to a monoploid. It is postulated therefore by those who hold the view of a double fusion that there is correspondingly a double reduction, and that this second nuclear reduction takes place in the third division in the ascus. The name **brachymeiosis** is given to this division.

In either case the mature ascus contains eight nuclei around each of which a wall is laid down, resulting in the formation of eight separate **ascospores** which are smooth and ellipsoidal.

The asci arising from each group of ascogonia are arranged side by side in a concave cluster or disc, around which the peridium forms a marginal layer, thus constituting an open ascocarp or **apothecium.**

In the meantime the sex organs themselves have disorganized and hyphae grow in from the apothecial sheath to form a layer of paraphyses lining the inner surface of the apothecium. As the asci mature they push their way between these paraphyses so that at maturity the lining layer of the apothecium, the **hymenium,** is composed of an intermingled mass of asci and paraphyses (Fig. 256). As this fruiting body matures it flattens out and the colour of the hyphae composing the hymenium changes from clear white through pale pink to salmon red, thus rendering it a very pretty little structure up to about 3 mm. in diameter. Since the sex organs are frequently produced quite close together on the mycelium, it follows that the mature fruiting bodies tend to run into one another, and *Pyronema confluens,* as the name implies, is generally found with its fruiting bodies in confluent masses.

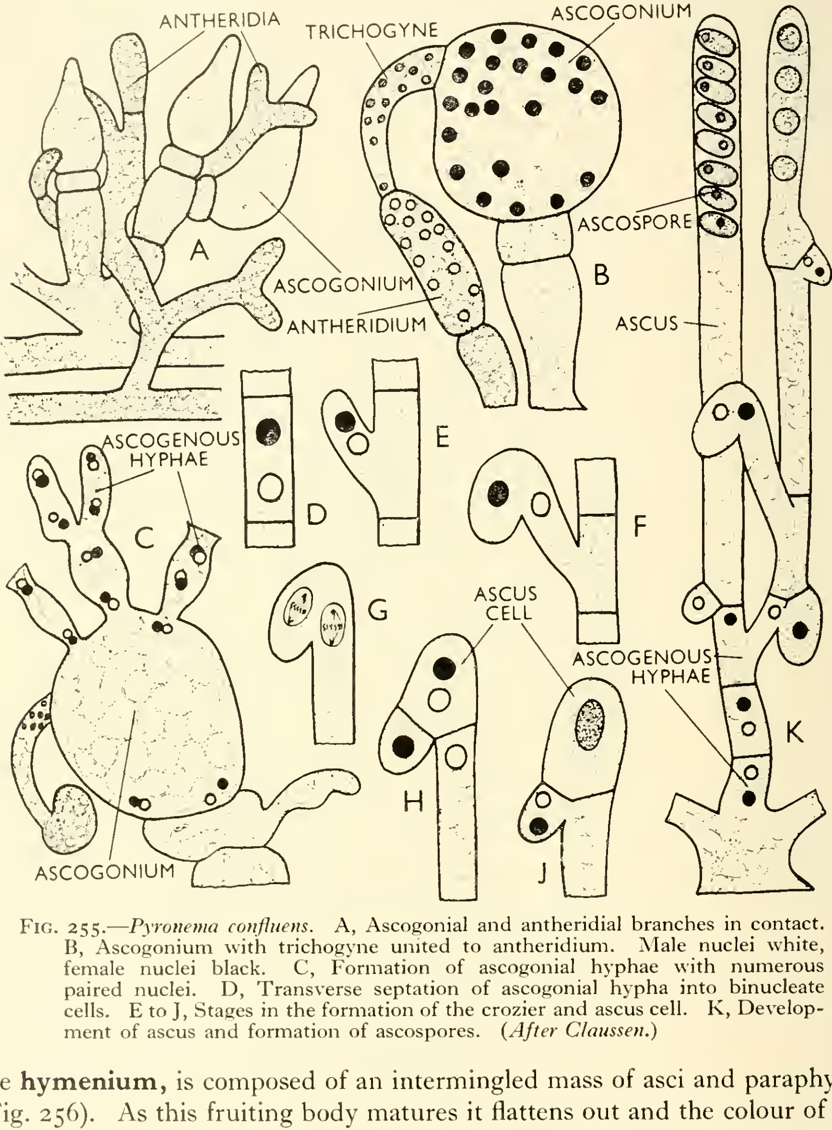

FIG. 255.—*Pyronema confluens.* A, Ascogonial and antheridial branches in contact. B, Ascogonium with trichogyne united to antheridium. Male nuclei white, female nuclei black. C, Formation of ascogonial hyphae with numerous paired nuclei. D, Transverse septation of ascogonial hypha into binucleate cells. E to J, Stages in the formation of the crozier and ascus cell. K, Development of ascus and formation of ascospores. (*After Claussen.*)

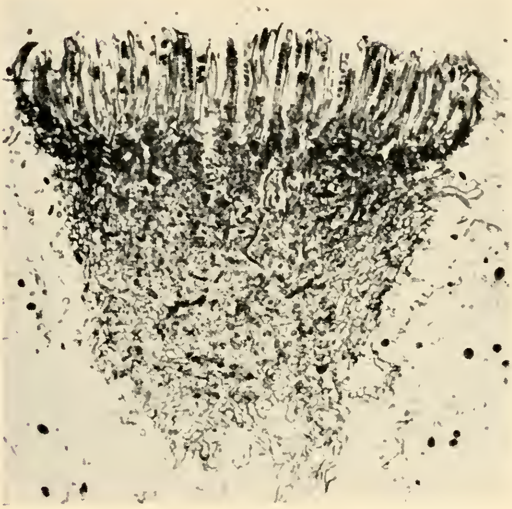

FIG. 256.—*Pyronema confluens.* Longitudinal section of mature apothecium.

Peziza vesiculosa

This Fungus is to be found growing on manure piles and on heavily manured soil, and on account of its large size is readily recognized. The cups are often irregular in shape and may become contorted (Fig. 257). The vegetative mycelium ramifies within the substratum on which it lives, forming a very complex system, through which food is absorbed by the fungus. The fruiting bodies either arise directly on the substratum, when they are

FIG. 257.—*Peziza vesiculosa.* Habit photograph showing the fruiting bodies growing on soil.

said to be **sessile,** or they may be elevated on a short stalk. Externally they are white or buff in colour, but the inside of the cup is brown. The outer surface is frequently covered by minute wart-like pustules, but the inside is smooth.

ASEXUAL REPRODUCTION

This type of reproduction occurs irregularly by the production of **conidiospores,** or by the formation of thick-walled spores, termed **chlamydospores,** which develop singly or in groups within the cells of the mycelium. Both germinate to produce fresh hyphae.

SEXUAL REPRODUCTION

Sexual reproduction in the Pezizales varies considerably. A series of types showing progressive reduction in the sex organs can be seen by a comparison of species. Firstly it appears the antheridium ceases to function, as we have already seen in certain species of *Aspergillus.* Then the trichogyne of the oogonium disappears, and finally the oogonium itself is not formed, but in its place certain cells of the vegetative hyphae take over its function and all that is left of the original sexual process is the fusion of two nuclei within a purely vegetative cell.

In *Peziza vesiculosa* the apothecium begins as a weft of tangled hyphae, and in the centre of this mass are certain cells which are said to possess nuclei which fuse in pairs. These cells then give rise to ascogenous hyphae. From these the asci are formed, and in them the ascospores are produced. There exists in this species the same question as to whether there are two fusions, the one of the paired nuclei in those vegetative cells which play the part of the sex organs, and the second fusion in the ascogenous hyphae, or whether there is only the second one. According to which view is adopted the last division of the nuclei in the formation of the ascospores will either be regarded as a reduction division or not. The ascospores are arranged obliquely in a row within the ascus, and each is ellipsoidal and smooth in outline.

The asci stand side by side forming a continuous layer over the inner surface of the apothecium. They are cylindrical and are intermingled with straight, slender hyphae, which are termed **paraphyses.** The special layer formed of the asci together with the paraphyses is termed the **hymenium** (Fig. 258). The eight ascospores are discharged from the ascus through a terminal aperture, only under damp conditions. Breathing on the surface of a ripe fruiting body will often cause the liberation of a cloud of spores. On germination they either produce a fresh mycelium, or they may give rise to a hypha from which conidia are developed.

Helvellales

The Helvellales are large Ascomycetes usually growing saprophytically on dead wood, in which the fruiting body is fleshy and in which the hymenium

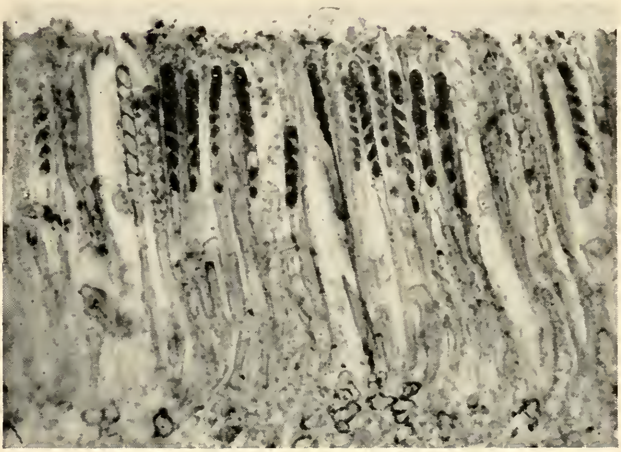

FIG. 258.—*Peziza vesiculosa.* Section through portion of apothecium with paraphyses and asci containing ascospores.

is spread over the external surface of the greater part of the fruiting body and covered at first by a membrane or veil. It seems probable that they have

FIG. 259.—*Helvella elastica.* Fruiting body. Natural size.

originated by the eversion of an apothecium which was already provided with a stalk. By development on a convex surface the hymenial layer is increased in area, and this is further increased by folding of the surface which may in some genera result in the formation of a very complex, convoluted head supported on a sterile stalk. Stages in this evolution can be traced in this order and, to a lesser extent, in certain Pezizales, with the result that it is not easy to draw a sharp line between them, and some authorities prefer to merge the Helvellales into the Pezizales. This view has certainly much to recommend it.

We shall consider one example of the order, *Helvella elastica*, though in most features it differs but little, so far as is known, from a number of allied species.

Helvella elastica

This Fungus occurs quite commonly in woods throughout Great Britain in company with a number of other species which differ mainly in colour and in the degree of fragmentation of the cap. Most of the species are edible and constitute the Morels of the mycophagist, though the true Morel (*Morchella esculenta*) belongs to a distinct genus.

Helvella elastica is usually white, though sometimes tinted with pale pink or grey. It is clearly divisible into a stalk or **stipe** and a cap or **pileus** (Fig. 259). The former is very firm, somewhat swollen below and deeply grooved. The cap is thin, somewhat lobed, with the lobes at first more or less attached to the stem, later becoming free. The Fungus occurs in moist places and is not uncommon in summer and autumn.

The mycelium consists of long, sparsely branched, interwoven hyphae, which show numerous anastomoses and may contain from two to many nuclei in each cell.

Development of the Fruiting Body

Here and there, by more vigorous growth, little knots of hyphae appear, the cells of which are thicker and shorter and the filaments more branched. These represent early stages in the formation of fruiting bodies.

Slightly later the main tissues of the fruiting body can be recognized, and in a knot of hyphae about 0·5 mm. in diameter it is possible to recognize a short thick stem passing insensibly into the mycelium below and surmounted by a bulbous cap, slightly larger in diameter than the stem. The whole structure is covered by a membrane. The membrane consists of two layers, an inner tissue termed the **palisade layer,** which is made up of the club-shaped ends of hyphae arranged close together to form an even surface. Outside this is an envelope formed from certain hyphae of the palisade layer which grow out beyond its surface, turn at right angles and grow over it. This envelope is transitory, breaking up at an early stage and then degenerating.

In the region of the cap **paraphyses** appear at quite an early stage. They force their way between the cells of the palisade layer, breaking the envelope

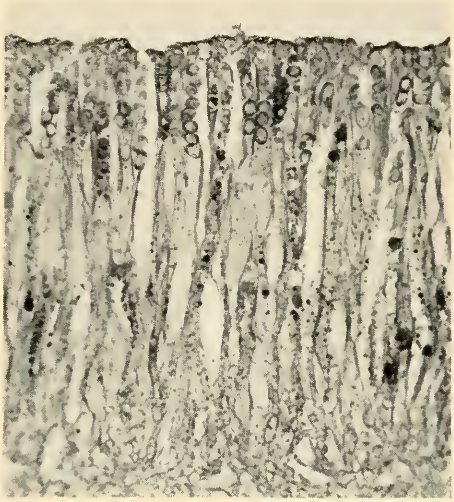

FIG. 260.—*Helvella elastica.* Section through hymenium showing asci containing ascospores.

as they do so. In this way a **hymenial layer** becomes differentiated on the surface of the cap (Fig. 260).

THE ASCOGENOUS HYPHAE

So far as is known no sex organs are produced. At a fairly early stage, however, some of the hyphal threads form a mat of tissue a short way below the paraphyses. These cells are multinucleate and considerably thicker than the ordinary hyphae. It is from these cells that asci are produced by

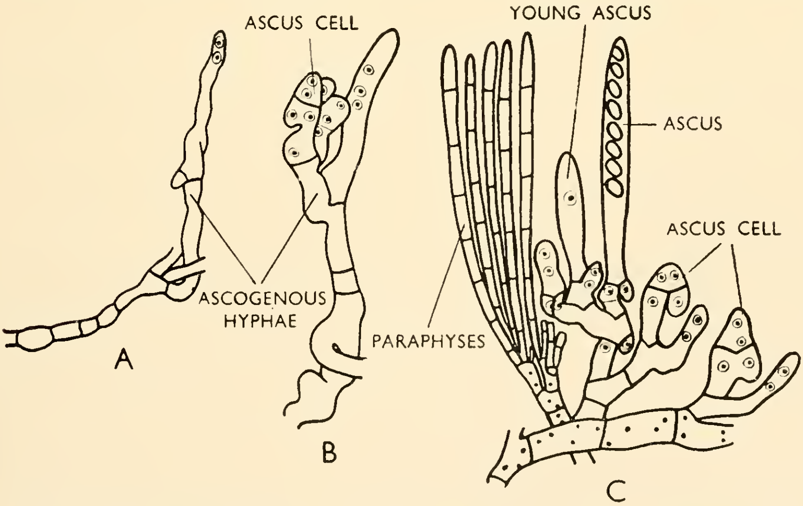

FIG. 261.—*Helvella elastica.* A and B, Development of ascogenous hyphae. C, Part of hymenium with paraphyses and developing asci. (*After McCubbin.*)

the vertical growth of branches from this sub-hymenial layer. The branches so formed divide repeatedly and penetrate between the paraphyses. The end cells of these branches contain deeply staining protoplasm and usually only two nuclei. These end cells curve over and form hooks, and in each hook the two nuclei divide into four. This is followed by the septation of the hook into a row of three cells. One nucleus enters the terminal cell, one the basal, and two remain in the middle cell. This middle cell enlarges and becomes the ascus, in which the two nuclei fuse (Fig. 261). Meiosis of the fusion nucleus follows and by a further division eight nuclei are formed, around each of which an ascospore is organized.

These ascospores are oval in shape and brown in colour. They are ejected forcibly from the apex of the ascus, and occasionally a tiny cloud of spores may be observed around a fruiting body when large numbers of ascospores are being expelled together.

It will be noted that the two nuclei which fuse in the ascus have been produced apogamously from vegetative hyphae and there is no evidence that any sexual apparatus is developed. By analogy with other types it may well be supposed that a hyphal fusion occurs somewhere prior to the production of a fruiting body, but work along this line has not yet been done.

Phacidiales

The Phacidiales are Ascomycetes in which the apothecia are immersed in the fungal tissue which is partly buried in the host tissue. They are generally small in size and of a leathery or corky consistency. The group is a small one but includes several genera which produce spots on the leaves of higher plants. It should be noted, however, that many of the common leaf-spot diseases are not caused by members of this order. Some of these diseases are caused by members of the Sphaeriales in which the ascocarp is flask-shaped, whereas in the Phacidiales it is more or less flat and widely open. Others, and indeed the majority of leaf-spot Fungi, are placed among the Fungi Imperfecti because they reproduce only asexually, by conidiospores.

We shall consider one example of this order, *Rhytisma acerinum*.

Rhytisma acerinum (The Black Spot Disease of Maples)

This Fungus is extremely common throughout the country, attacking the leaves of the common Field Maple and also the Sycamore ; in fact, few trees and indeed few leaves escape. Superficially these leaves appear to have been spotted with large drops of tar, and it seems that the lower leaves are usually more frequently attacked and have larger spots than those at the top of the trees. These black spots occur on the upper surface and average about 15 mm. in diameter (Fig. 262). They consist of a wrinkled **stroma,** roughly circular in shape, which is formed mainly in the epidermal cells of the leaf, though the hyphae spread down into the cells of the palisade layer as well.

The mycelium arises from a germinated ascospore which forms a germ tube and enters the leaf through the epidermis. It traverses the intercellular spaces of the palisade cells and also the spongy mesophyll.

In the epidermal cells the mycelium penetrates the cross walls repeatedly, so that the outer surface of the epidermal cells gradually becomes split away from the rest of the leaf. Meanwhile black material becomes deposited in between the epidermal cells, and the infected area changes colour from yellow to black.

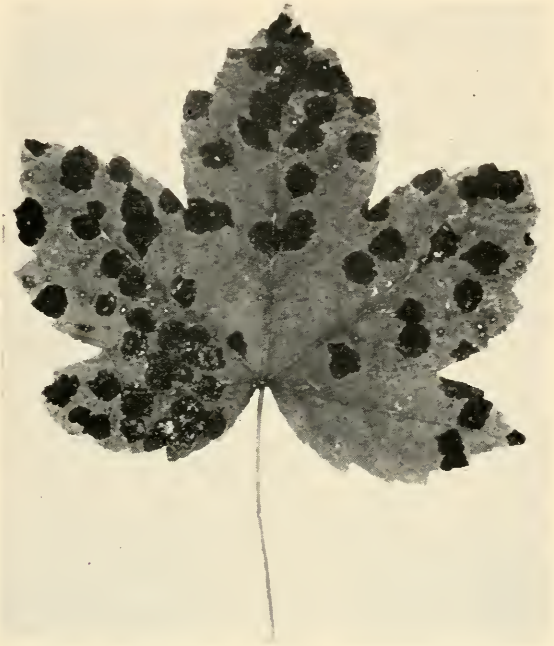

FIG. 262.—*Rhytisma acerinum.* Stromata on leaf of *Acer pseudoplatanus.*

ASEXUAL REPRODUCTION

At a fairly early stage in development it is possible to see the elaboration of the future asexual reproductive area by the modification of the part between the upper and lower walls of the epidermal cells (Fig. 263). Not only does the deposit of black material become denser along the lower surface but the mycelium gradually forms a continuous tissue in the bases of the cells and produces vertically growing hyphae, which extend upwards towards the upper walls of the epidermal cells. These elongating hyphae are really **conidiophores** and later abstrict **conidiospores.**

Meanwhile the mycelium from which the conidiophores arise becomes more dense and forms a closely interwoven tissue of small uninucleate cells termed a **plectenchyma.** Not only does this form the entire floor of the cavity, but circular ramparts grow up, dividing the area into a number of cavities which are for a time covered by the upper walls of the original epidermal

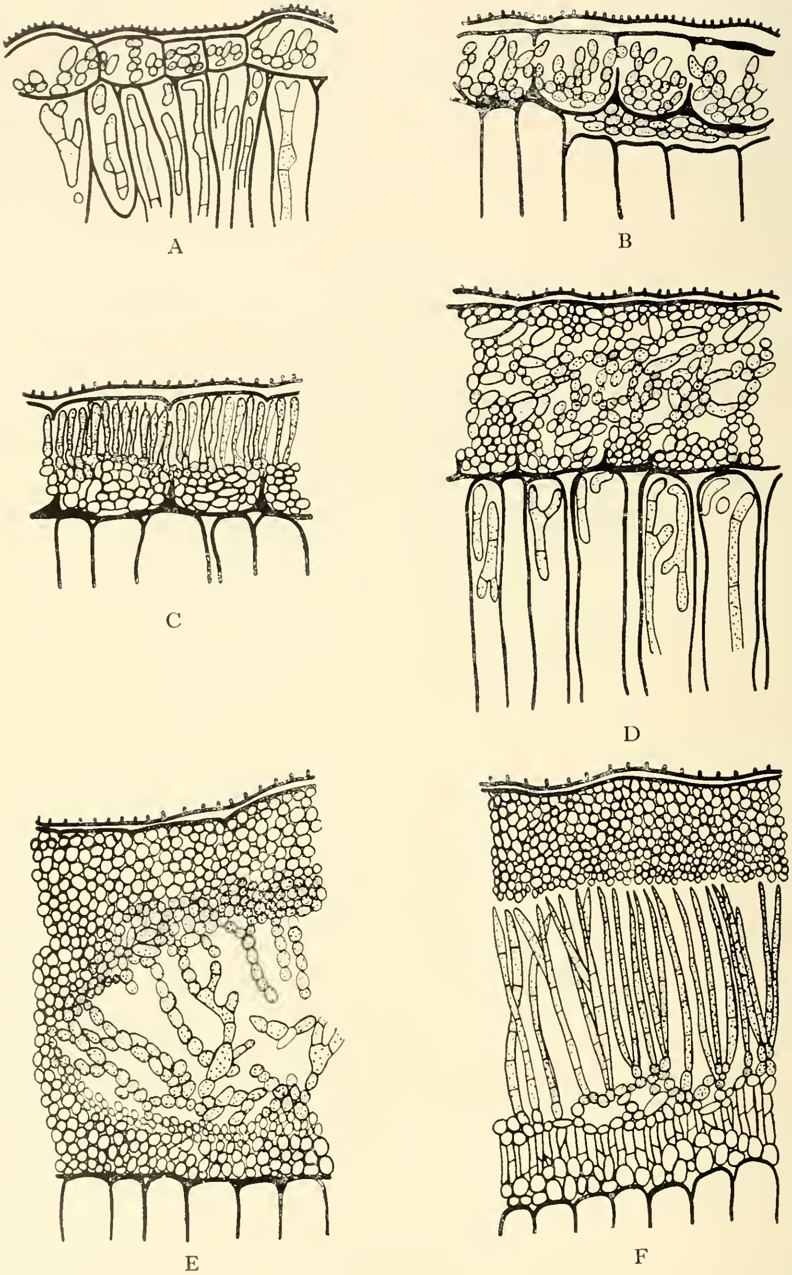

Fig. 263.—*Rhytisma acerinum.* A, Epidermis and palisade of leaf at early stage of infection. B, Early stage in formation of acervulus, rupture of epidermal walls and deposition of black substance. C, Later stage showing differentiation of basal plectenchyma and vertical conidiophores. D, Early stage in apothecial formation showing formation of upper and lower plectenchyma. E, Later stage of apothecium showing increased formation of roof plectenchyma. F, Apothecium with paraphyses among which the ascogonia are formed. (*After Jones.*)

cells, now completely disorganized. As these cavities enlarge vertically the conidiophores commence to cut off conidiospores in chains and fill the cavities, which eventually burst open by the breakdown of the upper epidermal walls. Such cavities, in which asexual conidia are produced, are termed **acervuli.** Despite the fact that these conidiospores are produced in vast numbers they have not been germinated under experimental conditions, and there is no evidence that they do actually spread the Fungus during the summer months when they are mainly produced.

Sexual Reproduction

The apothecia may be formed either in old acervuli or in newly formed cavities in the epidermis. During the autumn the plectenchyma becomes more sclerotic and blackens considerably. In the interior of the plectenchyma numerous apothecial cavities become differentiated. These become filled with loose hyphal tissue and are covered not only by the outer epidermal walls but also by a thick-walled black tissue called the **epithecium.** Below, the cavities rest on a somewhat lighter, thick-walled tissue, the **hypothecium,** which in turn covers the lower epidermal walls.

In each of these apothecial cavities the female sex organs are formed. Each consists of a uninucleate stalk cell, two or three multinucleate ascogonial cells and a uninucleate trichogyne. Apparently no male sex organ is formed and no true fertilization takes place. Instead, the septa between the ascogonial cells break down and their nuclei pair together.

Ascogenous hyphae now grow out from the ascogonium and paired nuclei migrate into them. The ascogenous hyphae branch repeatedly, and many asci are produced from a single ascogenous hypha. Each young ascus possesses a pair of nuclei derived by conjugate division from the original pair in the ascogenous hypha. These two nuclei then fuse.

The single fusion nucleus in the ascus now undergoes three divisions, resulting in the formation of eight nuclei, around which eight ascospores are formed. These ascospores are long and slender and lie side by side in a packet along the length of the ascus.

Meanwhile, from the loose hyphae in the apothecial cavity paraphyses are differentiated which grow up between the asci, so that at maturity the asci are more or less enveloped in a mass of very slender, elongated filaments.

The mechanism for bursting the apothecium is elaborate. Changes, mainly of the roof of the apothecial cavity, are initiated about the time that the asci begin to form. A layer of cells about three-quarters of the depth from the top break down, thus forming a small rift which gradually expands downwards, while at the same time the upper part of the roof rises and finally ruptures at the top (Fig. 264). At this stage the apothecium is closed only by the tissue below the rift. When the spores are ripe this too ruptures and the apothecial cavity is exposed. Some apothecia never open widely and the opening remains as a narrow fissure (Fig. 265), in others the roof bends back so that the whole cavity is exposed.

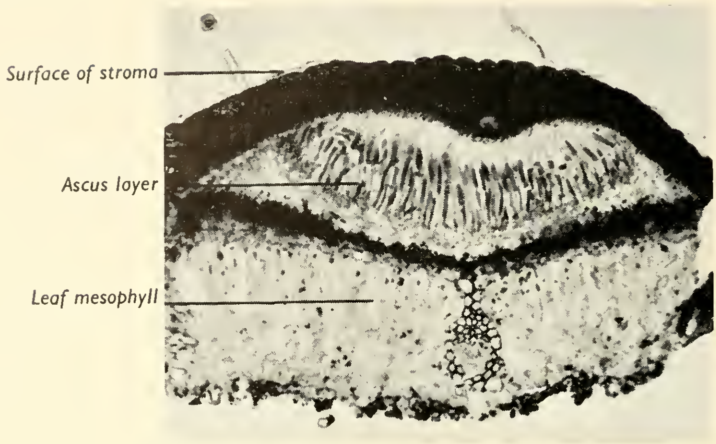

FIG. 264.—*Rhytisma acerinum.* Apothecium with developing asci showing beginning of rift in roof.

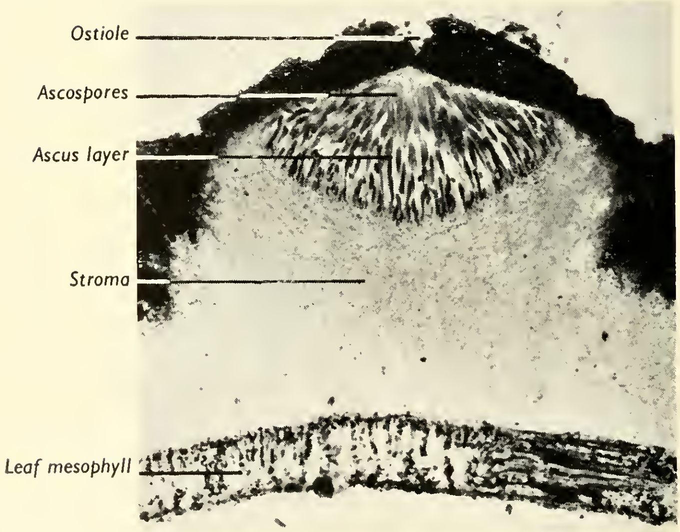

FIG. 265.—*Rhytisma acerinum.* Mature apothecium showing roof breaking open.

Since the development of the asci takes place during the winter it must obviously occur when the leaves have been shed, hence the discharge of the ascospores will take place in the early spring at a time when the leaf remains have largely rotted and the bits are blown about. In this way additional distribution of the Fungus is effected quite apart from the fact that the ascospores are forcibly ejected from the ascus. Moreover, as a result of contraction of the epithecium the ascospores may be shot up as much as 1 mm. above the surface of the substratum. They ultimately reach the young leaves as they unfold in the spring and there germinate to start the life-cycle over again.

Saccharomycetales

The organisms included in this order are of somewhat diverse character, but they are all predominantly unicellular. They have probably originated from more than one group of Fungi and are now classed together because of their similarity of form. We know that some Fungi which are not at all closely related to this order can adopt under certain conditions a yeast-like habit of growth, so that the unicellular condition may have been arrived at along more than one evolutionary line. It is at any rate reasonably certain that this feature is secondary or derived, so far as this group is concerned and not primitive in the evolutionary sense.

Some members of the order possess a definite sexual process, but in many it is wholly lacking. In the latter case reproduction is entirely vegetative. It may be that such species are really heterothallic, in which case the chances are very great against the two strains meeting to conjugate, except in artificial culture.

Saccharomyces cerevisiae (The Beer Yeast)

The cells of *Saccharomyces* are very minute and either spherical or slightly oval. They are about 10μ in diameter and are clothed with a delicate membrane, which appears to be a compound of two polysaccharides, glycogen and mannan, in combination with phosphoric acid. Cellulose is not present. There is abundant cytoplasm containing several small vacuoles in which are often grains of **volutin** (so called from its having been discovered in the bacterium *Spirillum volutans*), which is ribo-nucleic acid or one of its salts.

During fermentation glycogen increases in the vacuoles so that they stain dark brown with Iodine. This carbohydrate is the chief metabolic product and reserve material of the yeast cell.

The method of nuclear division is still uncertain, some authorities maintaining that it is entirely amitotic, while others claim the existence of a simple form of mitosis with two chromosomes. The latter view seems the more probable in view of the life-cycle described below (Fig. 266).

Species of yeast have been kept in cultivation by mankind since early times, and are widely used in fermentation processes, *e.g.*, in beers, wines and milks, and for baking. Many species are, however, to be found wild on the surfaces of higher plants, especially on the fruits. When the latter drop in autumn the yeasts pass into the soil where they spend the winter. In spring they are splashed by rain back on to the plants, thus completing the cycle. We will deal with the chemistry of the fermentation of sugars by yeasts under Respiration in Plant Physiology (Volume III.)

ASEXUAL REPRODUCTION

Reproduction in *Saccharomyces* takes place in two ways. The first is by the formation of **buds** on the vegetative cells, and the second is by means of

ascospores, the true nature of which is open to question. Budding takes place very rapidly when the food supply is abundant and is in many species the only known method of multiplication. A bud begins as a small protrusion of the wall of the mother cell, usually near one end, which rapidly enlarges until it is as large as the mother cell itself (Fig. 267). The junction of the two cells is by a very narrow neck, and buds are therefore usually detached easily. Sometimes, however, when growth is most vigorous a bud will itself produce another bud or buds before it is detached, so that a short chain of cells is formed. It is not infrequent to find that the young cells remain attached to each other and to the parent cell for some time, so that quite large

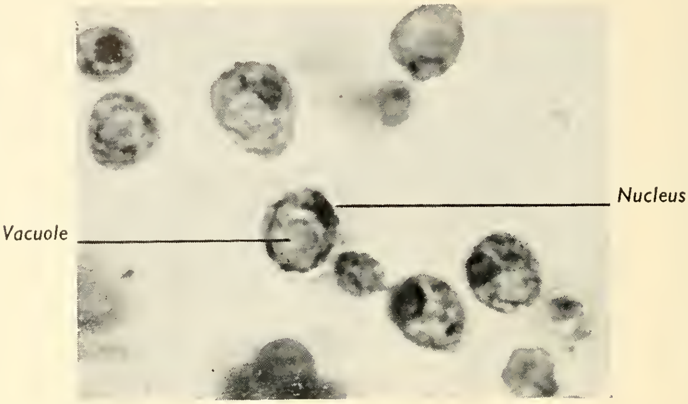

Fig. 266.—*Saccharomyces cerevisiae.* Photograph of cells stained to show nuclei and volutin grains.

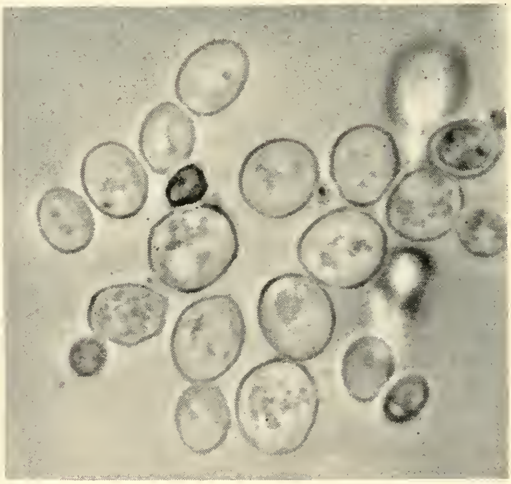

Fig. 267.—*Saccharomyces cerevisiae.* Vegetative cells showing budding.

groups may be found, containing up to a hundred cells, which remind us that the yeasts, although normally unicellular, may be closely related to types of Fungi which produce regular mycelia. When a bud is formed the nucleus of the cell divides and one portion passes into the bud, but whether this division is a mitotic process has not been fully established (Fig. 268).

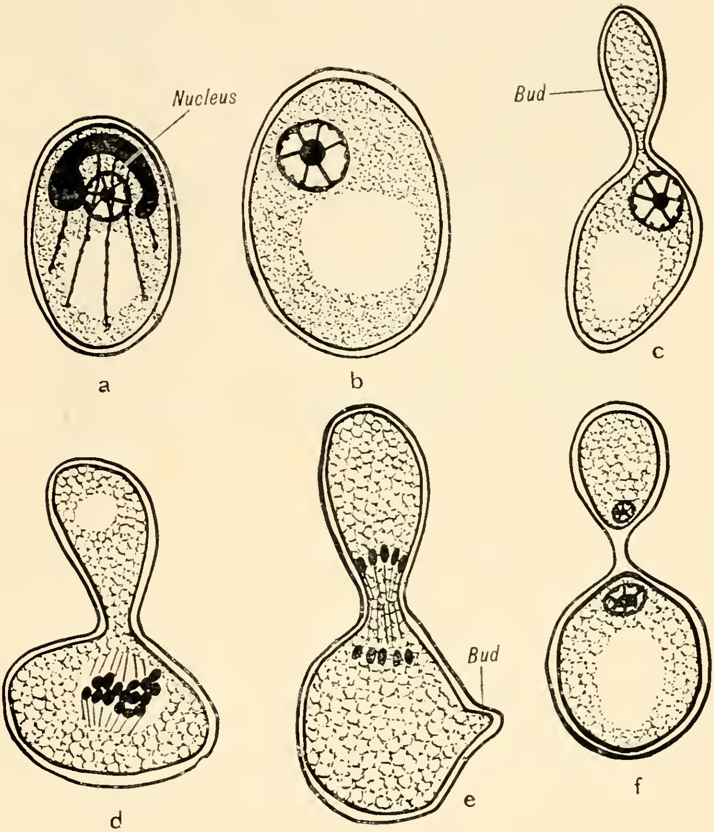

Fig. 268.—*Saccharomyces sp.* A and B, Structure of vegetative cell. In A, glycogen deposit shown black. C, Development of bud. D and E, Stages in mitosis. F, Separation of bud with daughter nucleus. (*After Kater.*)

Sexual Reproduction

Ascus formation occurs when the food supply, and especially when the water supply, is scanty. The commonest method of inducing the formation of asci is by sowing an active culture on a damp plaster block in a closed glass dish. Another way is to spread the yeast on a sterilized slice of carrot which is kept dry. The asci are slightly enlarged vegetative cells, the contents of which divide and round off into four ascospores with rather dense and highly refractive walls (Fig. 269).

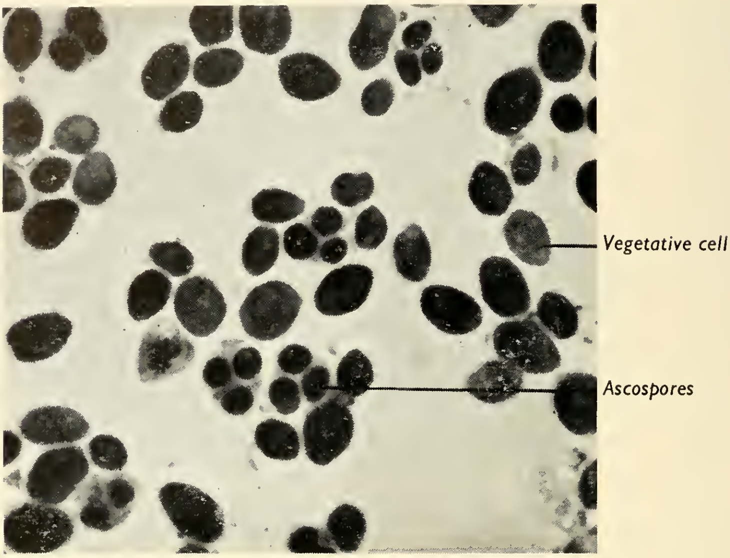

Fig. 269.—*Saccharomyces cerevisiae.* Formation of ascospores.

When an ascus breaks down the four spores germinate, and normally they fuse together in pairs with fusion of nuclei to produce two **zygotes** (Fig. 270), which start budding immediately and produce vegetative cells, which will in time give rise to asci again. It sometimes happens, however, that an ascospore germinates without conjugation, and in this case it gives

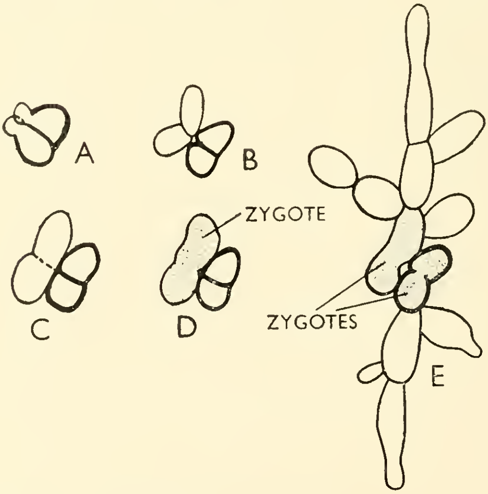

Fig. 270.—*Saccharomyces ellipsoideus.* A and B, Two germinating spores. C and D, Fusion of buds. E, A second zygote has been formed by the conjugating spores and both are germinating. (*After Winge.*)

rise to much smaller, almost spherical cells, which also multiply by budding and form a "dwarf" strain. These cells cannot produce asci until two of them have conjugated to form a zygote, which by budding produces the normal, large-celled strain again. Frequently many such conjugations occur simultaneously among the dwarf cells so that it would appear as if the dwarf strain had almost wholly turned into the large-celled strain (Fig. 271).

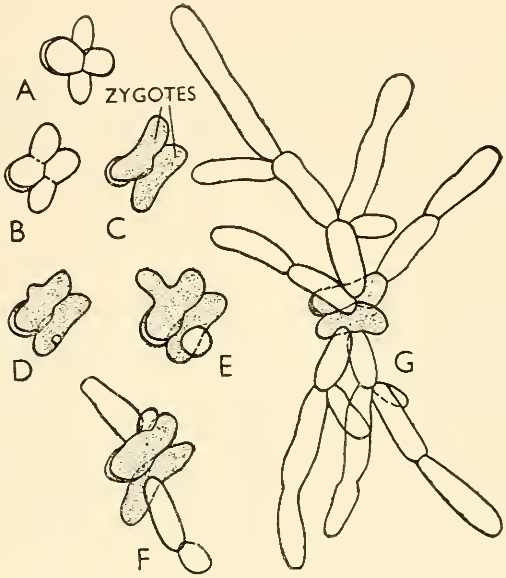

Fig. 271.—*Saccharomyces validus.* A, Monoploid spore with three buds. B and C, Twin zygotes formed by fusion. D to G, Development of diploid colonies from twin zygotes. (*After Winge.*)

These facts find their explanation readily enough when viewed as an alternation of generations. The normal large-celled strain is diploid, *i.e.*, is sporophytic, and gives rise to sporangia (asci) in which presumably meiosis occurs at spore formation. The ascospores would therefore, as in other cases, be monoploid. If they germinate singly they give rise to a small-celled gametophytic strain. This forms no definite sexual organs, but conjugation takes place, as in some other Ascomycetes, between vegetative cells, producing diploid zygotes, which reproduce the diploid strain once more. It happens, however, that in most cases the gametophyte phase is short-circuited, and the first cells produced from the germinating ascospores, instead of developing vegetatively, conjugate immediately to form a diploid zygote, so that the ascospores in such a case are the only monoploid cells in the life-cycle. Whether there is any advantage in such a procedure, or whether it merely is the result of the propinquity of the ascospores we cannot say, but we know that such short-circuiting of an alternating cycle does in fact occur in very various types of organisms, *e.g.*, in *Puccinia* among the Fungi ;

in *Fucus* among the Algae, and in the phenomenon of Apospory among Ferns.

The discovery of the conjugation between germinating ascospores in Yeast has opened up very remarkable and valuable possibilities of artificial hybridization, and already a considerable number of such hybrids have been created in the search for improved capabilities of fermentation.

Schizosaccharomyces octosporus

We may contrast the account of *Saccharomyces* with the condition in another member of the Saccharomycetaceae, *Schizosaccharomyces octosporus*. In this species the vegetative cells are more or less spherical and, like all yeasts, are capable of multiplication by budding. Under certain conditions, however, reproduction by a sexual process may occur. Two adjacent cells of similar size put out processes (Fig. 272) which come into contact and fuse, forming a **conjugation tube.*** The nucleus from each cell passes into the conjugation tube and there they fuse together. The two conjugating cells now enlarge, and eventually a single, large oval structure is formed, which is an **ascus** (Fig. 273). The zygote nucleus divides to form usually eight nuclei, around which **ascospores** become organized. Sometimes the remains of the conjugating cells can be distinguished after the formation of the ascospores, in which case four appear to lie in each of these cells.

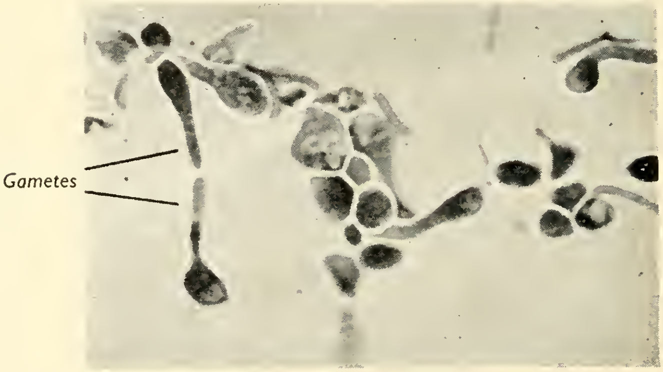

FIG. 272.—*Zygosaccharomyces sp.* Cells producing conjugating processes.

In this species, therefore, it is clear that the ascus is a post-fertilization structure agreeing in the method of its production with that of a typical Ascomycete, and there is some evidence that meiosis occurs during the formation of the ascospores. Hence in this type the true ascomycetaceous nature of the yeasts becomes more apparent.

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* Conjugation also takes place in some other yeasts, *e.g.*, *Zygosaccharomyces*, of which we give an illustration in the text. Note that the conjugating processes are much longer than in *Schizosaccharomyces*.

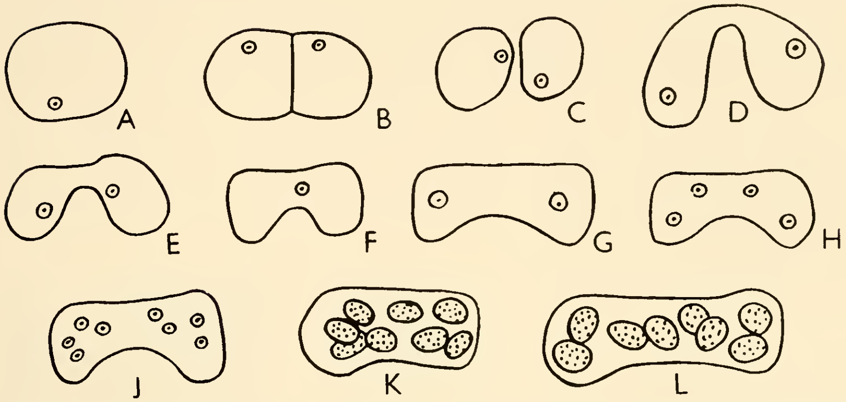

FIG. 273.—*Schizosaccharomyces octosporus.* A, Vegetative cell. B and C, Division of vegetative cell. D to F, Conjugation and formation of fusion nucleus. G to L, Development of ascus and formation of eight ascospores. (*After Guilliermond.*)

Hypocreales

The Hypocreales are Ascomycetes in which the asci are arranged in a perithecium which opens at the top by an ostiole. This perithecium is flask-shaped, and is either free or sunk in a stroma formed from the tissues of the Fungus. The asci usually produce eight ascospores which are generally hyaline, elliptical or filiform in shape, and may be composed of more than one cell. The stroma, and the perithecia when free, are often brightly coloured, red, yellow or purple being common shades.

The group includes a number of interesting species, some of which are of economic importance. Species of the genus *Nectria* form bright red stromata on the surface of wood, pushing up and cracking the bark in the process. On account of their colour and appearance these Fungi are called the Coral Spots, and at least one species causes a canker disease of fruit trees. Other members of the group live as parasites, mainly of tropical insects, the bodies of which become filled with the fungal mycelium until the creature is killed. The peculiar appearance produced as a result of the growth of the Fungus out of the body of an insect gave rise in earlier times to a belief that they possessed medicinal and magical value. *Cordyceps sinensis* on caterpillars, for example, was a celebrated drug in the Chinese pharmacopoeia.

We shall consider one example of this order, *Claviceps purpurea*, which causes a disease known as Ergot of Rye. The Fungus contains a powerful muscular stimulant and is still used for medicinal purposes.

Claviceps purpurea (Ergot of Rye)

The Fungus, though characteristic of Rye, also attacks other species of grasses (Fig. 274), including Wheat and Oats. There are several **biologic races**: *e.g.*, that growing on species of *Lolium* being incapable of infecting Rye and other cereals.

The ascospores are carried to the grass plants at the time when the flowers are maturing and find a lodgment among the floral parts. The hyphae formed from them penetrate and ramify in the ovary, where they form a thick mass of tissue, which becomes hard and purple on the exterior and forms a **sclerotium.** Meanwhile certain hyphae from within the tissues of the ovary grow outwards through the ovary wall and their exposed apices function as **conidiophores** and cut off small, spherical **conidiospores** (Fig. 275). The effect of this fungal infection is to cause the enlargement of the ovary, which at its upper end becomes rather spongy in character. During the development of the conidiospores a sugary secretion is produced by the hyphae. Insects are attracted to this " honeydew " and aid in distributing the conidiospores to other flowers where they can produce fresh sclerotia.

Fig. 274.—*Claviceps purpurea.* Flowering spike of *Avena pratensis* bearing a black sclerotium or ergot of the fungus in place of one of the flowers.

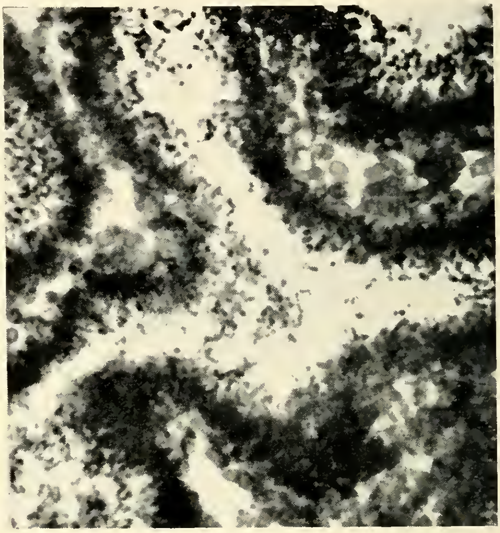

Fig. 275.—*Claviceps purpurea.* Formation of conidiospores.

Sexual Reproduction

After the conidial stage has reached its climax the sclerotium begins to mature. The hyphae in the base of the ovary, instead of forming a loose weft of filaments, become compacted into a dense mass which grows in length and finally projects an inch or more from the ear of rye, which has by this time ripened, carrying at its apex the remains of the mycelium which bore the conidia. In this process the ovary is completely destroyed and the sclerotium occupies its place, lying between the glumes of the rye spikelet.

This sclerotium is called the **ergot.** It is a hard body with a purple or black outer coat and a white interior. In this form the Fungus passes the winter, usually in the ground when the flower stalk has withered. In the spring it begins to grow by producing a number of fleshy stalk-like projections, each of which terminates in a globular head and is termed a **stroma** (Fig. 276). These stromata are yellowish-brown in colour. When mature the globular heads are seen to be covered with slightly raised papillae, surrounding pores which are really the ostioles of **perithecia.** In a longitudinal section through the head these perithecia will appear as flask-shaped cavities arranged in a single layer all over the surface of the head (Fig. 277).

Fig. 276.—*Claviceps purpurea.* Two sclerotia germinating to produce stalked stromata.
(*From the Museum of the Pharmaceutical Society, per Dr Wallis.*)

Fig. 277.—*Claviceps purpurea.* Longitudinal section through a stroma showing stipe and peripheral zone of perithecia.

The sex organs are formed in regular positions in the perithecial heads and produce a layer. Each originates from a single, elongated, multinucleated hypha which is rich in cytoplasm and arises from a vegetative cell. The terminal cell of this branch swells and the nuclei in it divide and arrange themselves in pairs, forming a **dicaryon.** From the positions of the nuclei, branches arise, each of which is unicellular and each receives a single dicaryon. This branch then elongates considerably and nuclear division ensues. The branches then bend towards one another in pairs, one of a pair being stouter and thicker than the other, which is slender and elongated.

The former functions as an **ascogonium,** the latter as an **antheridium.** On the side of the ascogonium nearest to the antheridium, a papilla is formed, the wall dissolves and the nuclei of the antheridium pass into the tip of the ascogonium.

The further development is uncertain, but apparently the nuclei pass to the base of the ascogonium, while the tip disorganizes and disappears. Later, in the position of the ascogonium, are seen binucleate cells, presumably derived from the ascogonium, which form **ascogenous hyphae.** The tips of these hyphae bend over, a terminal cell is cut off, and from the penultimate cell an **ascus** is formed in which the **ascospores** develop (Fig. 278).

Each perithecium contains a number of narrow, tubular asci which taper at either end. Each ascus encloses eight filiform ascospores. These ascospores are liberated through a small opening at the apex of the ascus. The ascospores can be carried by wind to the flowers of the rye, which, if they are open, receive them. It has been recorded that the ascospores are themselves capable of budding off conidiospores which will also infect the ovaries of rye plants. Thus the life-cycle is completed and we can represent it by the following diagram (Fig. 279) :—

Fig. 278.—*Claviceps purpurea.* Perithecium enlarged showing wall enclosing asci and paraphyses.

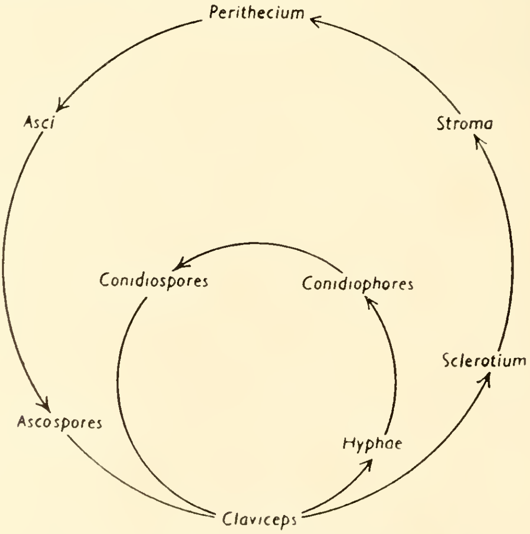

Fig. 279.—Life-cycle of *Claviceps purpurea.*

Economic Importance of Ergot

The occurrence of ergot in rye bread may have serious consequences, causing gangrene and loss of hair, teeth and nails. Cattle eating ergot grain may show gangrenous and nervous symptoms with the loss of hoofs, tails and horns, and miscarriage of young. Ergot poisoning, known as Ergotism, is very dangerous, the mortality being as high as 50 per cent.

Ergot is chiefly collected in Spain, Portugal, Poland and Russia, either by hand picking or by threshing through a special machine. Ergot contains Ergotamine and Ergotoxin, and is used medicinally to induce contraction of the smooth muscles, especially of the uterus in childbirth, and to control uterine haemorrhage (see Volume IV, Economic Botany).

Ergot contains, in addition to the above toxins, the substance acetyl choline, which causes muscular contraction in dilutions as high as 1 part in 500 millions. Acetyl choline is responsible for normal muscular contraction, being formed at the junction of the motor nerves and muscles, where it lasts for only a fraction of a second, producing contraction before it is destroyed by the enzyme cholinesterase. If its action is prolonged it causes paralysis.

Artificial infection of rye has been successfully accomplished in Vienna and also in Australia, though it still remains to be seen whether this can be done on a commercial scale.

Sphaeriales

The Sphaeriales are Ascomycetes in which the ascospores are produced in flask-shaped perithecia which are free or immersed in dark-coloured membranous or corky stromata. When the perithecia are immersed in a stroma they retain a distinct wall. Asexual reproduction is by conidiospores.

The group is a very large one ; the majority are saprophytes and are responsible for bringing about primary decay of plant tissues. Many produce leaf-spots, and it is only among the higher members that a large independent fruiting body is produced. This fruiting body may vary greatly in form from a spreading crust somewhat similar to a leaf-spot, to a spherical mass, while in a few examples the fruiting body consists of a simple or branched body of quite considerable size.

In such forms perithecia are developed just below and at right angles to the surface of the stroma, but it frequently happens that the asci are developed in cavities identical in shape to the perithecia, but in which chains of conidiospores had been previously produced. On the other hand, conidia may arise superficially both on the surface of the fruiting body and also on the mycelium itself. In the former position they may give a characteristic colour to the fruiting body.

We shall select as our example *Hypoxylon coccineum*, belonging to the Xylariaceae, the highest family of the Sphaeriales.

Hypoxylon coccineum

The fruiting body appears as a bright brick-red stroma, about $\frac{1}{2}$ in. in diameter, which may be produced singly or, more often, in clusters together. These clusters are formed upon the bark of dead deciduous trees, particularly beech, and occur during the summer and autumn (Fig. 280). When young the stroma is at first covered with fairly long, branched tufts of flattened, olive-brown conidiophores which are covered with **conidiospores.** During the later part of the summer these conidiospores disappear and the colour of the stroma becomes more clearly red. The **perithecia** are developed as a layer just below the surface covering the whole fruiting body. When mature each opens by a small, somewhat raised ostiole. The ascospores, eight of which are produced in each ascus, are oval in shape and brown in colour.

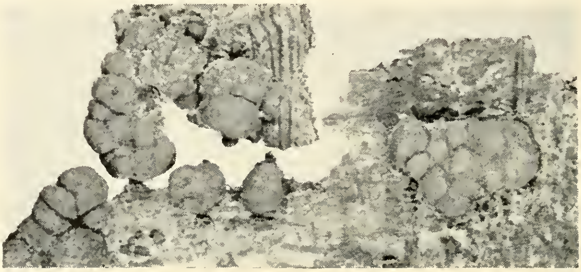

FIG. 280.—*Hypoxylon coccineum.* Stromata on Beech bark, about half natural size.

A vertical section through the stroma shows it to be differentiated into four zones, which can be seen in a stained section with the naked eye. The innermost zone consists of a loose arrangement of hyphae emerging from the substratum on which the Fungus is growing. Secondly, there is a dome-shaped mass of closely compacted hyphae which lie radially parallel to one another and are made up of empty cells. This zone forms the main mass of the fruiting body and supports the third zone which comprises the perithecial layer of loosely woven hyphae in which the perithecia are developed, each being surrounded by a much more closely fitting mass of cells similar to those in zone two. Finally, there is a fourth zone which forms a superficial layer, differentiated into three parts. Firstly, there is a line marking off the fruiting zone by interwoven hyphae which run parallel to the surface of the stroma. This takes a very dark stain. Secondly, there is a space occupied by loose hyphae with dense protoplasmic contents and, thirdly, a surface layer of closely packed hyphae which stain black, and from which at an earlier stage the conidiophores arose.

In the central region of zone two in the young state, it is possible to make out three distinct types of hyphae which appear to perform separate functions. The most conspicuous are those composed of long, large cells which are coloured brown. Besides these there are small hyphae with dense protoplasmic contents and still smaller ones which do not stain so densely. It is from the first of these types that the tissue of the stroma becomes differentiated, while the second type eventually gives rise to the perithecia, and the third type forms the superficial layers and the conidiophores.

The rigidity of the stroma is greatly increased by a system of interlocking effected by the large-celled hyphae. Despite the mechanical rigidity obtained in this way the walls of these cells are no thicker than those of the smaller hyphae which form the reproductive bodies.

On the edge of this central zone the small hyphae pass out into the perithecial zone. Those which are larger in diameter, however, do not continue beyond the inner part of this zone, while the very fine hyphae continue beyond it into the fourth zone, where they give rise to the superficial boundary.

Asexual Reproduction

Some of the thin hyphae of the superficial zone instead of forming a layer running parallel to the surface, grow outwards to the exterior. These hyphae are binucleate and somewhat flattened, and are made up of elongated cells. Each hypha branches once or twice and gives rise to conidiospores which are developed in clusters (Fig. 281). The conidiospores are small, oval and colourless. They are liberated in great numbers during the summer months and give rise to fresh mycelia.

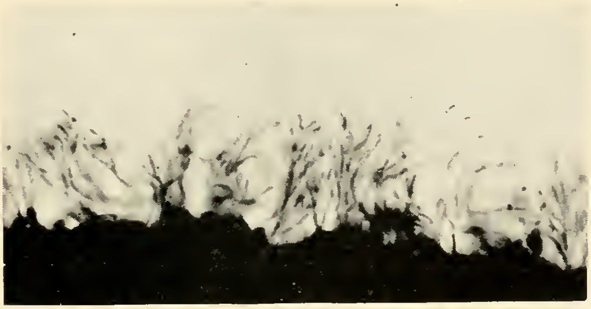

Fig. 281.—*Hypoxylon coccineum*. Section through stroma showing superficial conidiospores.

Conidiospores are not exclusively produced on the surface of the stroma. They are also produced as outgrowths directly from the mycelium. In addition, it is not unusual to find conidiospores developing inside young perithecia or possibly in those which would otherwise fail to mature.

Sexual Reproduction

The first indication of the formation of a perithecium is the coiling up of the end of one of the small hyphae lying in the lower region of the perithecial zone. Other hyphae soon grow and surround the coil, thus forming a small circular knot of tissue. As growth continues in the inner tissue the cells which will form the wall of the perithecium not only increase in size but additional hyphae grow up between the pre-existing ones. Thus the wall enlarges while at the same time a cavity develops between the ascogonium and the wall, probably as a result of the breakdown of the inner hyphae to provide food for the developing sexual apparatus (Fig. 282). Many perithecia begin to develop, although only some mature, and since these enlarge till they reach the peripheral zone while those which fail to develop do not, it follows that there appears to be a progressive development of perithecia from the centre outwards.

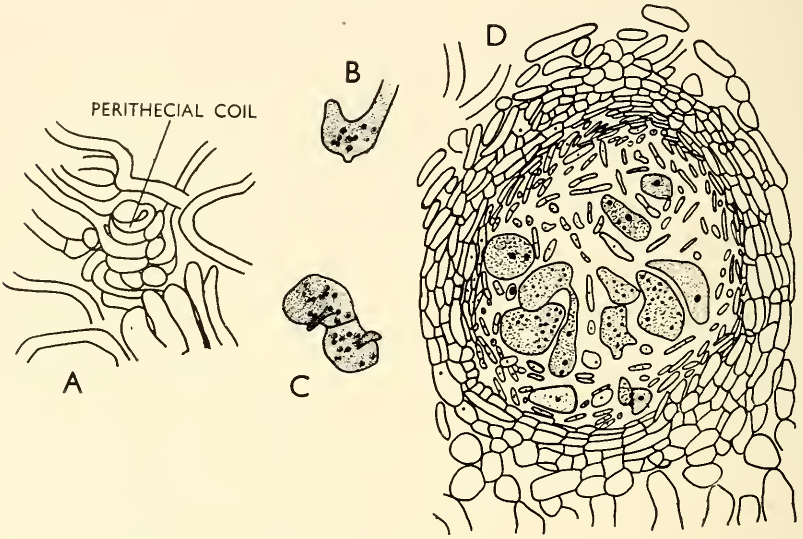

Fig. 282.—*Hypoxylon coccineum.* Development of the perithecium. A, Surface view of coiled hyphae. B and C, Budding of ascogenous hyphae from ascogonium. D, Section through perithecium with developing ascogonia. (*After Lupo.*)

Inside the young coil there appears a row of broad cells which are irregularly rolled up and full of protoplasm. This is termed the **Woronin hypha.** It increases in length, size and in the number of its cells. Certain of these cells enlarge and eventually separate from one another to form separate **ascogonia.** They enlarge very greatly, assuming quite irregular shapes and apparently contain many nuclei.

The basal wall of the perithecium now grows upwards into the cavity from below, so that the ascogonia become embedded in the floor of the perithecium, and here they continue to develop. From these ascogonia ascogenous hyphae are budded out, and into them nuclei from the ascogonia migrate.

The further development of the ascogenous hyphae into asci has not been followed, but by analogy with other groups it is reasonable to assume that they are formed by the branching and ramification of the ascogenous hyphae over the floor of the perithecium. Meanwhile paraphyses develop and separate the asci from one another. They are simple unbranched hyphae, and it is suggested that they may arise not from the wall tissue of the perithecium but as sterile branches from the ascogenous hyphae.

When mature the asci are long and slender, but are considerably shorter than the paraphyses, which partly fill the perithecium. Each ascus gives rise to eight ascospores which are oval in shape and brown in colour (Fig. 283).

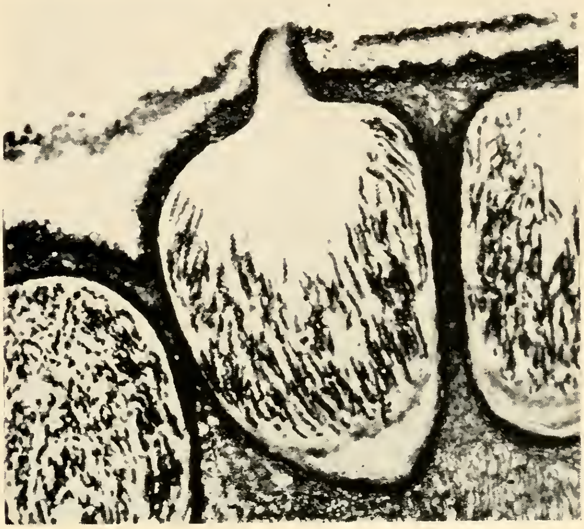

FIG. 283.—*Hypoxylon coccineum.* Section through mature perithecium showing asci with ascospores and ostiole of perithecium. Note the basal layer in which the ascogonia are embedded.

Meanwhile the wall of the perithecium has continued to develop, forming a thick plectenchyma of small cells containing, especially on the side nearest the cavity, dense black material. The perithecium is finally extended through the superficial zone as a short beak terminating in an ostiole. The inner margin of the ostiole is beset by short thin-walled filaments of cells which form a protective tissue between which the ascospores finally escape. They germinate to produce a fresh mycelium.

RELATIONSHIPS

Hypoxylon coccineum is among the most highly specialized of the Sphaeriales. It indicates the way in which, from a relatively simple type where the perithecia are embedded in the host tissues, as are the apothecia of *Rhytisma acerinum*, a complex external stroma is developed which protects and nourishes the developing perithecia and enables a very much greater spore output to be produced. It is worth noting that in certain allied genera *e.g.*, *Xylaria*, the size of these stromata is considerably greater than in the type we have selected. The family is essentially a tropical one, and the genera attain their highest development under such conditions.

Laboulbeniales

The Laboulbeniales are parasitic Ascomycetes living externally on insects. Though they may produce slight irritation they never cause the death of the host, in fact their survival ultimately depends upon the continued life of the insect, since with the death of the host they too are killed.

Though the members are small in size and consist merely of a filament of cells, the group is of great interest because of the structure of the reproductive organs. These consist of an ascogonium provided with a terminal trichogyne, and antheridia each of which liberates a single non-motile spermatium. These spermatia are carried passively to the trichogyne to which they become attached. As a result of fertilization a diploid nucleus is formed in the ascogonium which develops into an ascus from which four ascospores are ultimately produced.

We shall consider as our example of the group *Stigmatomyces baeri*.

Stigmatomyces baeri

The organism occurs on the common House Fly (*Musca domestica*) (Fig. 284) and was first investigated from material collected in Vienna.

The vegetative part of the organism, which is termed the **receptacle,** consists of the two superimposed cells of the ascospore, the upper cell giving rise to a multicellular **appendage** on which the antheridia are developed unilaterally. The lower cell of the receptacle divides obliquely and the cell thus cut off develops laterally into a perithecium. The perithecium is brownish-yellow in colour and contains a single row of cells, terminating in a single-celled trichogyne. After fertilization a single ascus is formed from the lowest cell but one of the filament and four ascospores are produced which are each divided into two cells.

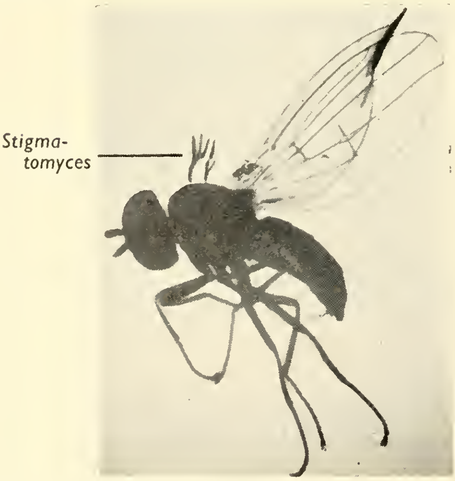

Fig. 284.—*Stigmatomyces spiralis*. Habit of growth of fungus on the body of a House Fly.

From a photograph from Thaxter's original preparation in the Farlow Herbarium taken by Professor Weston.)

Our knowledge of the development of this organism is due to the work of Thaxter, who, while working in the Harvard laboratories in Cambridge, Mass., U.S.A., investigated many members of this order and finally published the only comprehensive monograph of these organisms. The following account therefore is taken from this monograph.

The ascospores are fusiform in shape and are enclosed in a gelatinous sheath. Each spore is divided into two cells of unequal size, and the gelatinous wall is particularly well developed around the larger cell which lies toward the tip of the ascus before it is discharged. When this discharge takes place this larger cell with the gelatinous mass attached to it comes into contact with the integument of the insect and soon becomes firmly fixed thereto. This constitutes the receptacle referred to above.

The Antheridium

At this stage (Fig. 285) the organism consists of two cells, a large basal cell (1) and a smaller upper cell (2). The basal cell now cuts off a small cell which becomes the **foot** (1.1). The upper cell meanwhile divides into two cells by an oblique wall which is followed by a second similar oblique septum, thus forming three cells (2.1), (2.2) and (2.3). The lowest of these cells (2.1) now cuts off a wall perpendicular to the original one, thus dividing the cell into a large basal cell (2.1.1) and a small apical cell (2.1.2). This apical cell grows rapidly upwards pushing the cells (2.2) and (2.3) to one side. These two cells now divide in the same way cutting off apical cells, as may be seen in Fig. 285, forming (2.2.2) and (2.2.1) and (2.3.2) and (2.3.1) respectively, while at the same time a new cell (2.4) is cut off at the top from cell (2.3). Subsequently this cell also cuts off an apical cell (2.4.2) from a basal cell (2.4.1). In addition to this the top cell (2.5) remains undivided and curved downwards by the growth of the intermediate cells.

It will thus be seen that from the original upper cell (2) a group of five **antheridia** are produced, from the apical cell of each of which a tiny non-motile body is produced which is the male gamete or **spermatium.** It is a naked protoplasmic body, which is liberated from the antheridium and is carried passively to the female organ.

The Ascogonium

The **ascogonium** arises from the basal cell (1.2) of the original receptacle. It divides first into two cells (*a*) and (*b*). The upper cell remains small and forms the base of the **appendage,** while from the lower cell the future ascogonium is formed. Cell (*b*) now divides into a large basal cell (*b*.1) and a small apical cell (*b*.2). The latter again divides forming two cells (*b*.2.1) and (*b*.2.2). The further divisions are not entirely constant and we need not follow them in detail.

The development of the ascogonium takes place by the evolution of a cell mass derived from the original apical cell (*b*.2.1), which will now be referred to as cell (*c*) for simplicity. This cell grows upwards and divides into (*c*.1) and (*c*.2). Of these two cells (*c*.2) now divides by a longitudinal septum to form two cells (*c*.2.1) and (*c*.2.2). The latter cell (*c*.2.1) now divides transversely into two cells : (*s*) which divides no further and becomes the stalk of the perithecium, and (*p*) which forms the perithecial wall. At the same time cell (*c*.2.2) divides by a transverse wall into two other cells, (*s*.1) and (*p*.1), the former gives rise to the stalk of the perithecium, while (*p*.1) contributes to the wall of the perithecium. By further division of the cells (*p*) and (*p*.1) a two-layered perithecium wall is finally produced as may be seen by the subsequent diagrams, and the actual cell divisions need not be followed in detail.

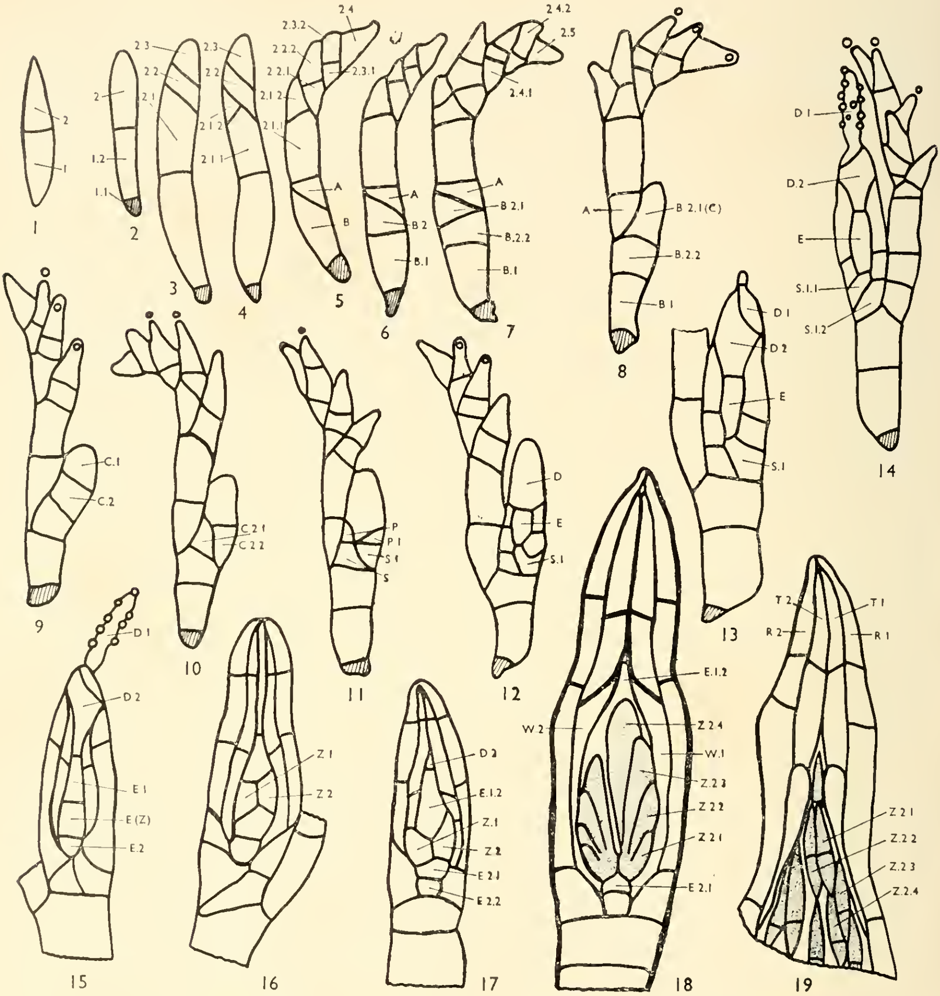

FIG. 285.—*Stigmatomyces baeri*. Stages in the development of the organism. For details see text. (*After Thaxter.*)

The cell (*c*.1) divides into two cells (*d*) and (*e*), which are surrounded by cells of the perithecial wall. Cell (*d*) divides into two (*d*.1) and (*d*.2). In this way a row of four cells are formed, which, starting from the tip, are termed respectively the **trichogyne** (*d*.1), the **trichophoric cell** (*d*.2), the **ascogonium** (*e*), and the **stalk cell** (*s*.1), which then divides again into two cells (*s*.1.1) and (*s*.1.2).

The development of this sexual apparatus now continues by the elongation of the tip of the trichogyne, forming a receptive part at the top, beset with numerous small swellings to which the spermatia become attached. Though the details of the process of fertilization have not been observed, it is concluded that at least one nucleus from a spermatium passes into the trichogyne and makes its way down towards the functional female nucleus situated in the ascogonium, for shortly after the final development of the ascogonium the trichogyne withers and disappears. The further development of the ascogonium consists in the cutting off of two subsidiary cells, one above (*e*.1) and one below (*e*.2).

The fusion of nuclei in the ascogonium transforms the ascogonium into a zygote and stimulates the zygote cell (*z*) to divide into four cells, two of which (*z*.1) and (*z*.2) are shown; while at the same time cell (*d*.2) becomes narrower, due to the division of the cells of the perithecial wall, which now becomes two layers thick, and a second supporting cell (*e*.2.1) is also formed by the division of (*e*.2).

The four cells (*z*.1), (*z*.2), (*z*.3), (*z*.4) now function as **ascogenous hyphae,** in so far as each produces a row of four asci, *e.g.* (*z*.2.1), (*z*.2.2), (*z*.2.3) and (*z*.2.4). In each ascus eight nuclei are formed during which presumably a meiosis occurs. In some genera an ascospore is constituted around each nucleus, but in *Stigmatomyces baeri* and most genera, four of these nuclei abort and only four spores are produced, *e.g.* (*z*.2.2.1), (*z*.2.2.2), (*z*.2.2.3), (*z*.2.2.4).

Fig. 286.—*Chitonomyces paradoxus.* Entire plant with branch on left terminating in mature perithecium and branched appendages arising from the receptacle.

(*From a photograph by Professor Weston.*)

By pressure of these developing asci the cells (*e*.1.2) and (*e*.2.1) together with the cells of the inner perithecial wall (*w*.1) and (*w*.2) become disorganized and destroyed, along with the ascus wall, with the result that the ascospores come to lie freely in the perithecial cavity. They are finally liberated between the cells at the apex of the perithecium (*r*.1) and (*r*.2), while the inner cells (*t*.1) and (*t*.2) are destroyed.

RELATIONSHIPS

The discovery of these Fungi naturally stimulated the view that the Fungi as a whole were derived from the Algae, for it was maintained, quite reasonably, that both the development of the female reproductive organ and also the presence of non-motile spermatia were features remarkably similar to those seen in many of the Rhodophyceae of the present day. Moreover, the fact that similar female organs and also spermatia, though apparently not functional, occur in certain Lichens, emphasized that the Laboulbeniales were not alone in possessing these Algal-like characters.

Despite these similarities, however, most mycologists now prefer to consider that the Laboulbeniales have in reality been derived from simpler Fungi.

BASIDIOMYCETES

The Basidiomycetes are Fungi consisting of a septate filamentous mycelium which ramifies either through the host tissues, in the case of parasitic species, or in the soil in many saprophytic ones, and produces highly complex fruiting bodies. The club-shaped cells which bear the spores are called **basidia,** and these may be formed either over the whole surface of the fruiting body or localized on certain special structures. From the **basidium** four spores, **basidiospores,** are externally developed. These, when they fall to the ground, form fresh mycelia. The mycelium which grows from a spore is composed of uninucleated cells. When two mycelia of different strains meet, a cell fusion takes place and a **secondary mycelium** is formed consisting of binucleate cells. In many species fruiting bodies are formed only on secondary mycelia, and all the cells of the fruiting body are binucleate. Sexual union consists in the fusion of the two nuclei in the basidium. This fusion is immediately followed by meiosis, so that the basidiospores are monoploid and uninucleate.

Asexual reproduction, where present, is by means of conidiospores borne on the mycelium.

Many of these Fungi are of economic importance in causing plant diseases. Many form mycorrhiza with the roots of trees, a factor which influences the ecological distribution of both partners in the association (see Volume IV).

The Basidiomycetes are divided into a number of orders, of which we shall consider examples of the following :—

1. **Urediniales** (*e.g.*, *Puccinia*).
2. **Ustilaginales** (*e.g.*, *Ustilago*).
3. **Aphyllophorales** (*e.g.*, *Polyporus*).
4. **Agaricales** (*e.g.*, *Psalliota*).
5. **Gasteromycetales** (*e.g.*, *Cyathus*, *Phallus*).

Urediniales

The Urediniales are Basidiomycetes in which the basidia are formed as outgrowths from a special type of spore. The life-cycle is complicated by the production of a number of different spore-types which succeed one another. They are all obligate parasites, mostly on the tissues of higher plants. In many types two dissimilar host plants are involved in the life-cycle, and there is a definite alternation of spore-types from one host plant to the other.

As an example of the group we shall consider the life-history of *Puccinia graminis*, the common Rust of Wheat.

Puccinia graminis (The Black or Stem Rust of Wheat)

This Fungus illustrates the condition known as **heteroecism,** in which the life-cycle of the species involves two distinct host plants. The alternate hosts in this case are the Wheat plant (*Triticum vulgare*) and the Barberry (*Berberis vulgaris*). A hundred years ago this Rust was a serious plague of wheat fields in Britain, but the removal of Barberry bushes, following upon the discovery of their part in the life-cycle of the parasite, has reduced its attacks almost to insignificance.

Life-history of the Fungus

It will be convenient to start the life-history with the **basidiospores,** which are carried by wind to the leaves of the Barberry in early spring. There the spore germinates and the primary hypha penetrates into the epidermis directly (Fig. 287). From there it branches freely, forming a uninucleate, monoploid mycelium between the cells of the mesophyll.

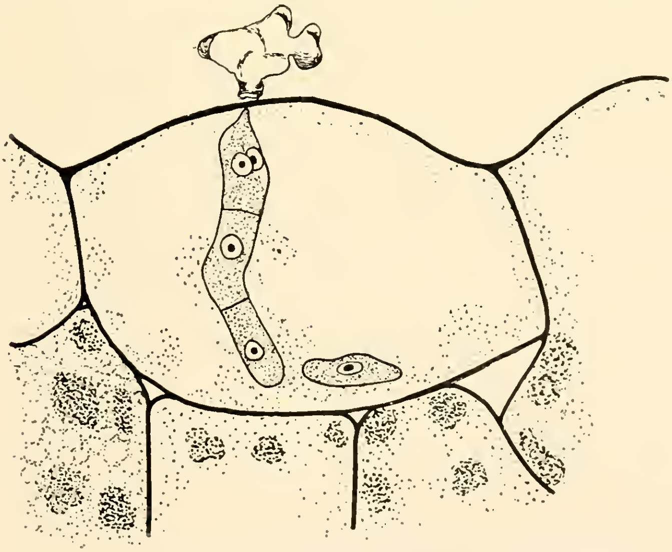

Fig. 287.—*Puccinia graminis.* Germination of basidiospore infecting leaf of Barberry. (*After Allen.*)

The Fungus is heterothallic, and the basidiospores are either of (+) or (−) strain. Although multiple infections of a leaf by basidiospores may occur, the two strains of mycelia can co-exist in the leaf, at least for some time, without fusion, each remaining monoploid. Fusion occurs later.

Four days after infection the mycelia produce **pycnidia,** mostly on the upper surface of the infected patch or pustule on the leaf. These are small flask-shaped bodies, inside which **pycnospores** are produced, by abstriction from short hyphae, along with **paraphyses** (Fig. 288).

The pycnidium secretes a sugary nectar which oozes out in a drop from the neck on to the leaf surface. The pycnospores, like the mycelia from which they spring, are of (+) or (−) strains. Fertilization is accomplished by mixing nectar, containing pycnospores of one strain with the exuded drop of nectar over a pycnidium of opposite strain. The older interpretation of the function of the pycnidia was that they were male organs producing male cells, and they were therefore called spermogonia and spermatia respectively. The female organs were supposed to be trichogynes formed by certain hyphae which penetrate outwards to the leaf surface. It is doubtful, however, if these supposed trichogyne hyphae are ever functional, and certainly the usual portal of entry for the " fertilizing " strain of the Fungus is through the existing pycnidia.

The transfer of nectar containing pycnospores from leaf to leaf is chiefly the work of flies which feed on the nectar. Shortly after a pycnidium has received spores of opposite strain, there must presumably be a fusion of pycnospores in the pycnidium, because hyphae grow from it in which the cells contain two or three nuclei. This is the diploid or sporophytic mycelium, which also ramifies through the mesophyll (Fig. 289). Fertilized pycnidia then dry up and die.

Meanwhile the primary or monoploid mycelium has built up, on the lower side of the leaf, spherical masses of cells which are the beginning of the **aecidia** or " cluster cups " (Figs. 290 and 291). If only one strain is present in the leaf these abort and die, but if a diploid mycelium reaches the young aecidium, its cells mingle with the monoploid tissue already formed and produce a tissue in the base of the aecidium from which the **aecidiospores** are developed (Fig. 292). The sporophytic cells become multinucleate, and from them binucleate spores are cut off terminally in chains, thus using up all the extra nuclei but two, which remain in the basal cell of the chain. Each mother cell of an aecidiospore, as it is cut off, divides and the upper half becomes the spore, while the lower half, which is called the **intercalary cell** soon disorganizes. The wall of the aecidium splits open and the spores are exposed in the cup thus formed. In an aecidium, therefore, the wall tissues are monoploid and the spore-forming cells are diploid. The orange colour of the aecidial cups makes them very conspicuous on the lower surface of the infected leaf.

The aecidiospores infect Wheat plants or other grasses, germinating on the leaves and sending inwards a primary hypha, generally through a stoma.

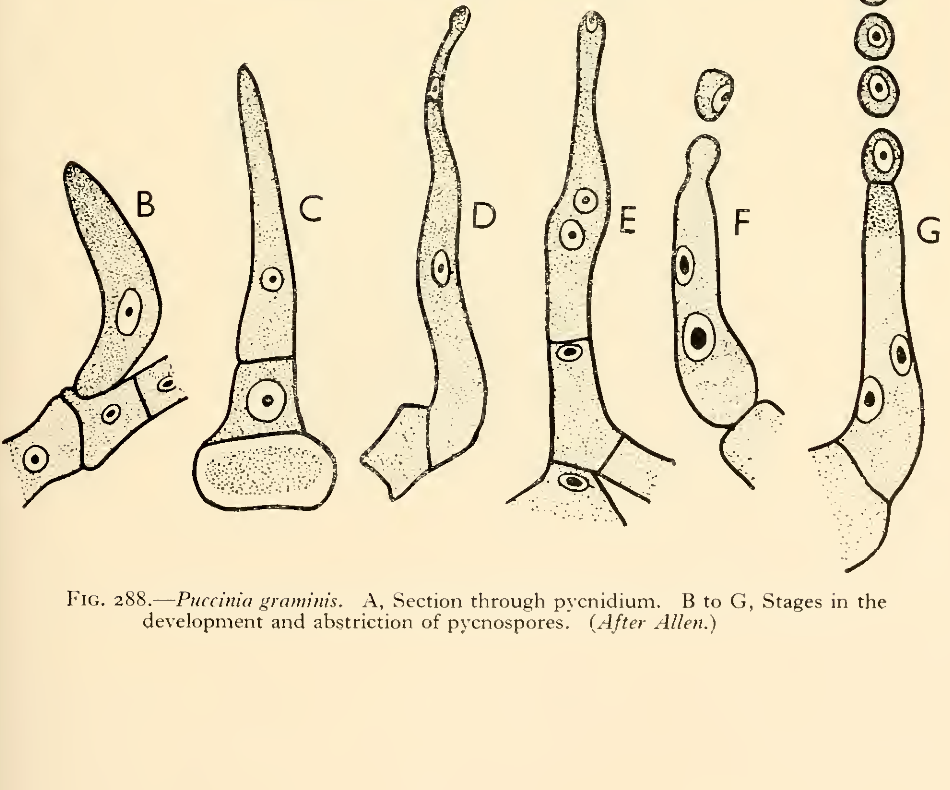

Fig. 288.—*Puccinia graminis*. A, Section through pycnidium. B to G, Stages in the development and abstriction of pycnospores. (*After Allen.*)

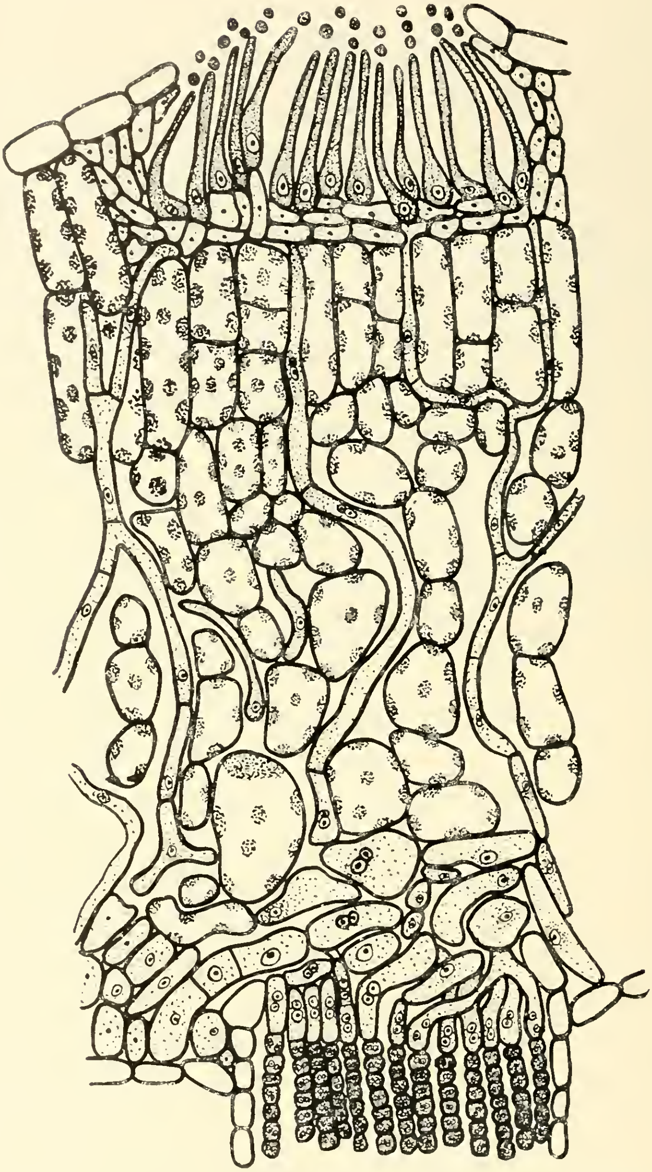

FIG. 289.—*Puccinia graminis.* Old pycnidium on upper surface of leaf from which diploid mycelium has penetrated to lower surface of leaf, where it has given rise to aecidiospores. (*After Allen.*)

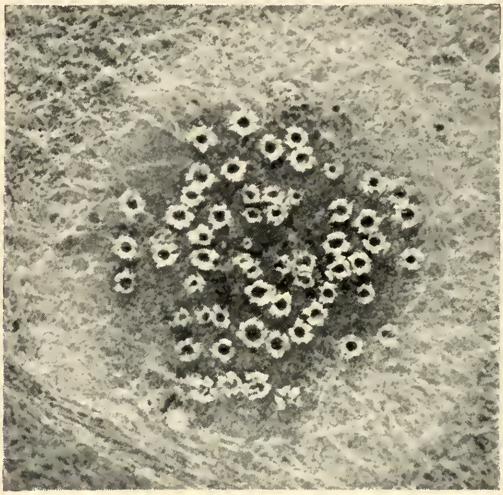

FIG. 290.—*Puccinia poarum.* Group of cluster cups in surface view on leaf of *Tussilago farfara.*

FIG. 291.—*Puccinia graminis.* Transverse section of leaf of Barberry showing pycnidia on upper surface, and aecidia on lower surface, discharging aecidiospores. The tissues of the leaf are hypertrophied.

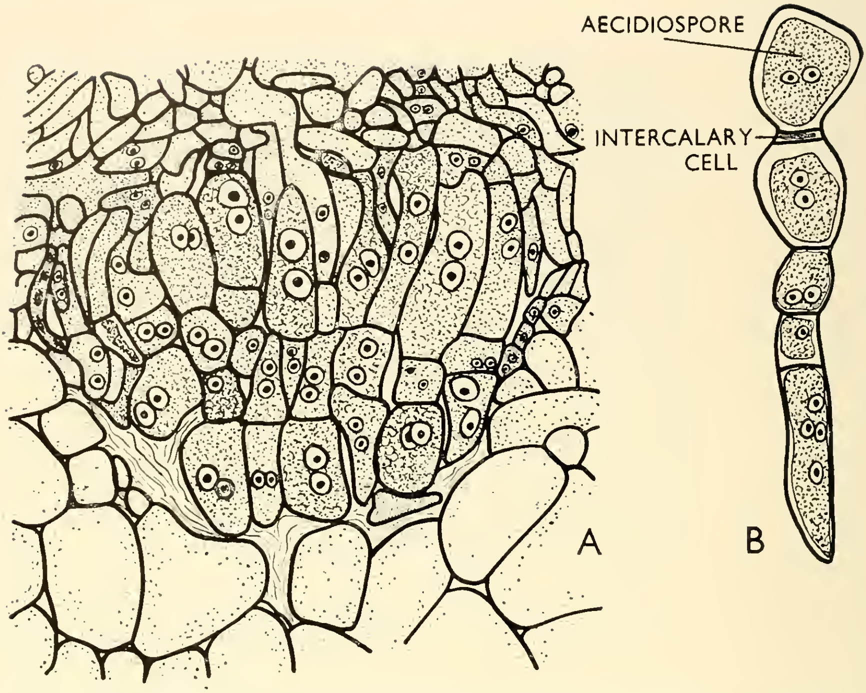

Fig. 292.—*Puccinia graminis.* A, Development of the aecidial hyphae in the base of the aecidial cup. B, Development and abstriction of aecidiospore. The aecidiospore is binucleate. (*After Allen.*)

As in the Barberry leaf the mycelium in wheat is chiefly intercellular. Only minute haustoria enter the cells. All this mycelium is diploid, in the sense that each cell contains a pair of nuclei which regularly divide together and are termed **conjugate nuclei** or, more briefly, a **dicaryon** (Fig. 294). After a few days the mycelium begins to form **sori** (Fig. 295) of yellow, binucleate spores called **uredospores,** which burst through the leaf epidermis in lines, which are from a few millimetres to several centimetres long. These spores are produced in the summer (Fig. 293) and are only able to reinfect other grass plants. They are oval in shape and have a warty cell-wall (Fig. 296). Towards the end of summer there appears among the uredospores another kind of spore of a dark-brown colour, the **teleutospore** (Fig. 297). These increase in numbers until by late autumn they have replaced the uredospores entirely (Fig. 298). Teleutospores are smooth-walled and spindle-shaped. Each divides transversely into two cells. In each cell are two nuclei which fuse when the spore is mature. Thus we see that the conjugate nuclei, which came together at the formation of the aecidium, do not fuse until the production of the teleutospores. The teleutospores when shed may lie upon the ground for some time, and do not usually germinate until the spring. Each cell has a **germination pore** in its wall, and from this grows out a short hypha. Into this there passes the fused nucleus from the cell of the teleutospore. This nucleus divides twice,

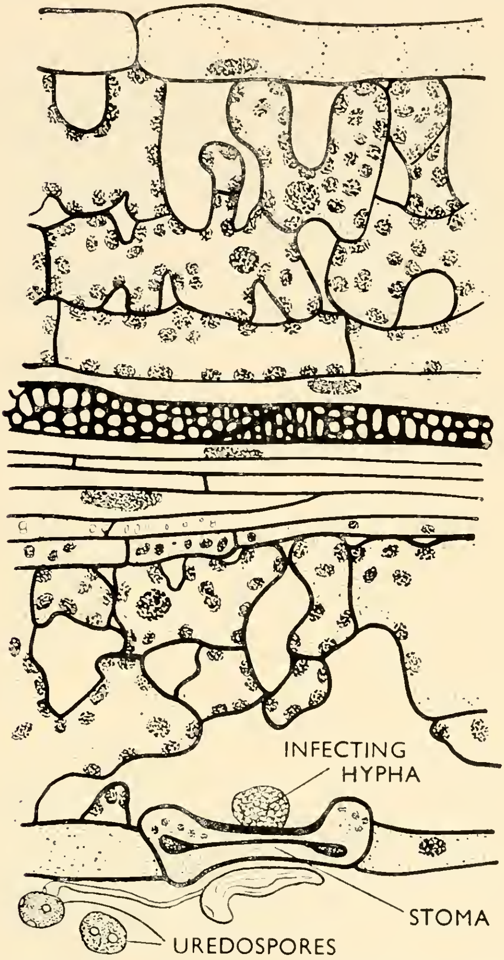

Fig. 293.—*Puccinia graminis.* Germination of the Uredospores on Wheat leaf and the entry of the germ tube through a stoma. (*After Allen.*)

during which meiosis occurs, producing a row of four monoploid nuclei, which are then separated from each other by transverse walls. This four-celled structure is termed the **basidium** (Fig. 299). It is comparable to the basidium in the Agaricales, but differs in being transversely septate, whereas in the latter case it is non-septate.

From the side of each of the four cells a short, narrow tube or **sterigma** grows out, on the end of which a single basidiospore develops and the monoploid nucleus from each cell passes through the sterigma into the developing spore. The sexual character is apparently segregated at the first nuclear division in the basidium so that two of the basidiospores are of (+) strain and two of (−) strain. They are carried by wind to the leaves of the Barberry and begin the cycle again (Fig. 300).

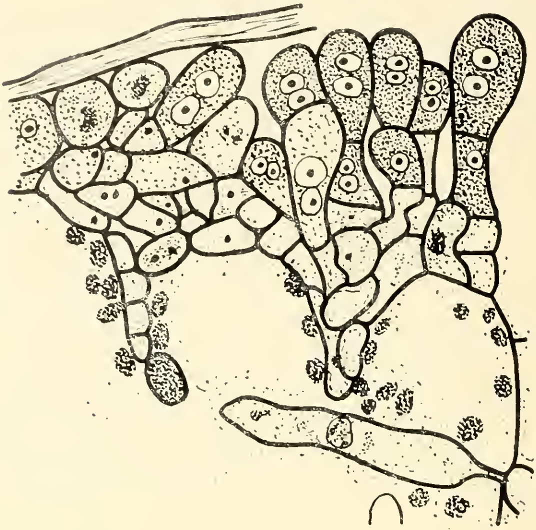

FIG. 294.—*Puccinia graminis.* Early stage in the formation of the uredosorus and the development of uredospores. (*After Allen.*)

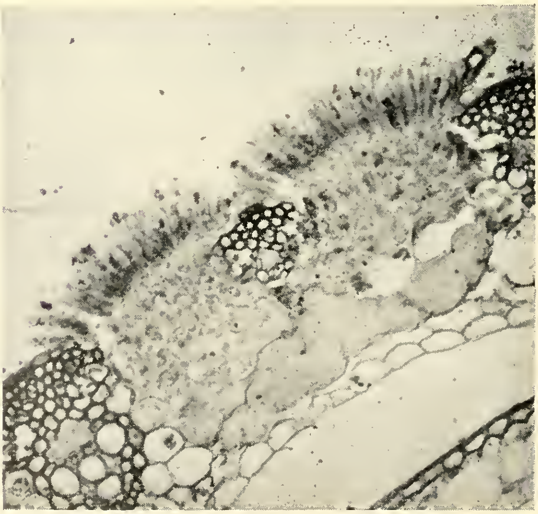

FIG. 295.—*Puccinia graminis.* Section of Wheat leaf with uredosori.

FIG. 296.—*Puccinia graminis.* Mature uredosorus with terminal uredospores. (*After Allen.*)

HOST RELATIONSHIPS IN THE RUSTS

Not all species of Rusts require two host plants to complete their life histories. In some all the stages in the life-cycle are passed through in a single host plant. Thus we can contrast *Puccinia graminis,* which is **heteroecious,** with those in which there is only one host, a condition said to be **autoecious.** In cases where there are two host plants it is usually found that these plants belong to families of very different systematic position, the one bearing the pycnidia and aecidia being usually of a less advanced type than that on which the uredosori and teleutosori are formed. Thus the Barberry belongs to the Berberidaceae, a family closely allied to the Ranunculaceae, which is considered a primitive family of Dicotyledons, while the grasses belong to the Gramineae, a specialized family of the Monocotyledons. There are many similar examples among the Rusts. The common Rust of the Nettle produces its aecidia and pycnidia on *Urtica dioica,* a primitive Dicotyledon, but its uredospores and teleutospores are formed on *Carex pendula,* a

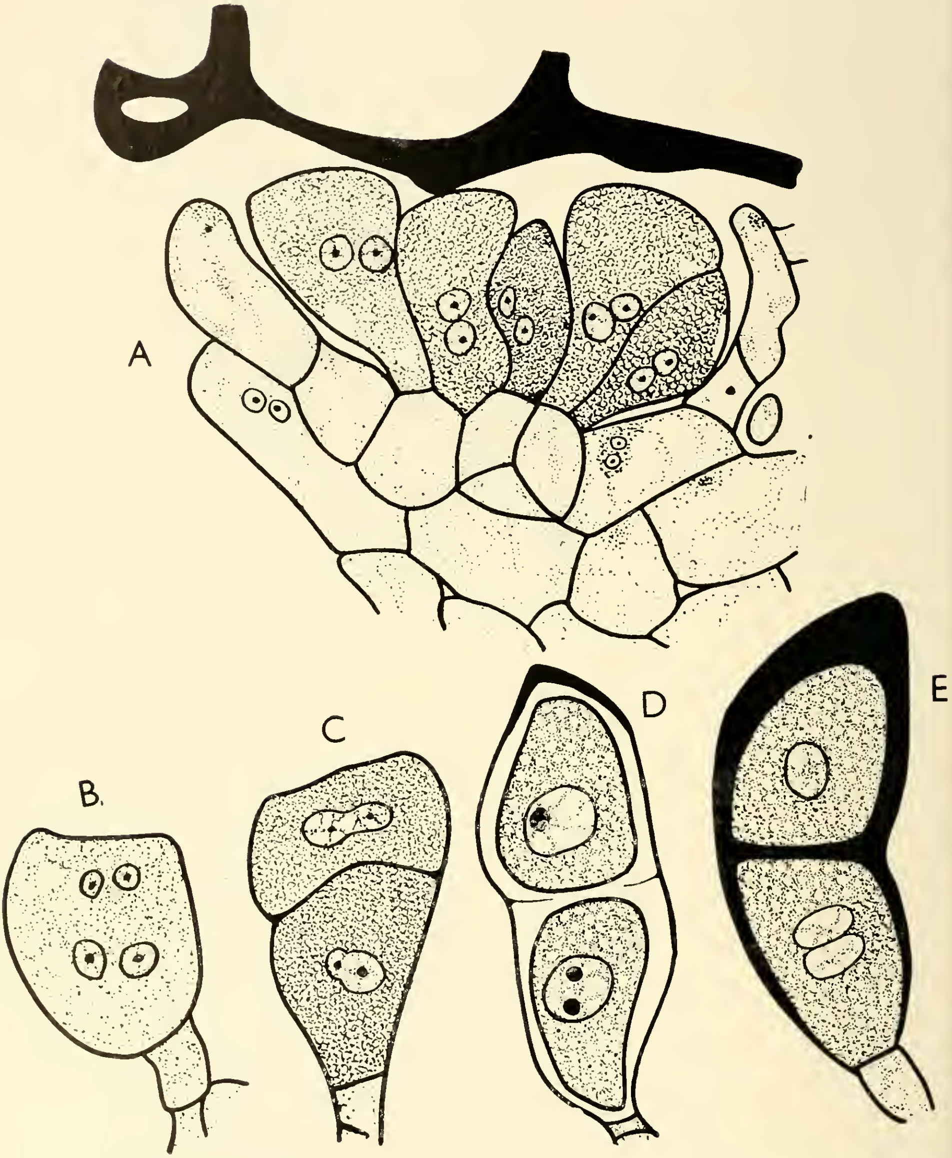

Fig. 297.—*Puccinia graminis.* A, Development of teleutosorus. B, Division of paired nuclei. C, Septation of cell and fusion of conjugate nuclei. D and E, Development of mature teleutospore. (*After Allen.*)

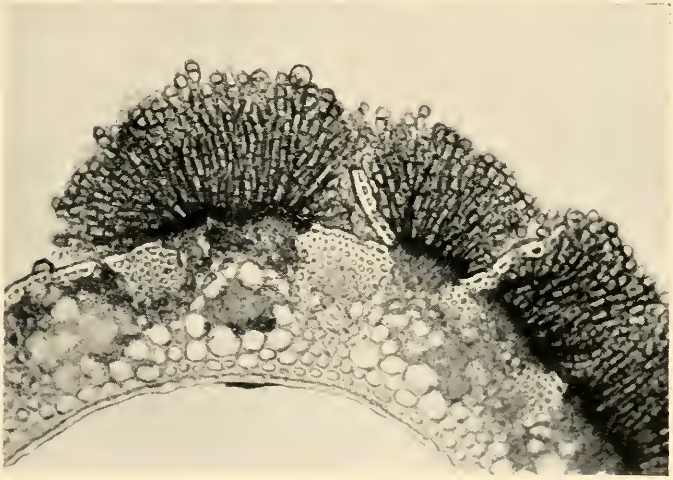

FIG. 298.—*Puccinia graminis.* Section of Wheat leaf with mature teleutosori.

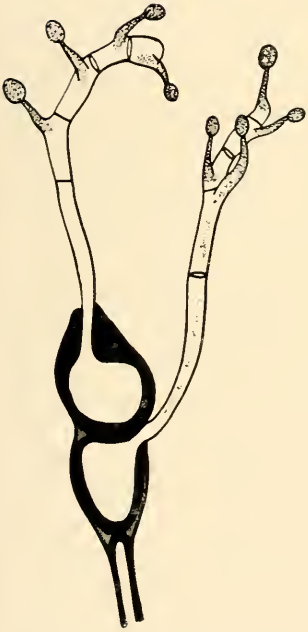

FIG. 299.—*Puccinia graminis.* Germination of teleutospore to produce two four-celled basidia which give rise to basidiospores.

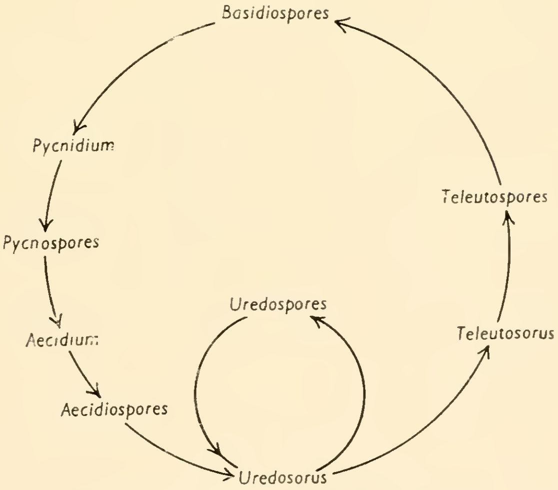

FIG. 300.—Life-cycle of *Puccinia graminis.*

specialized Monocotyledon. It must not be assumed by this that all Rusts alternate between Dicotyledons and Monocotyledons, though this is frequently the case. There are many which occur only on Dicotyledons, while others occur on Ferns. It must be noted, however, that the two host plants normally grow near each other.

There are many examples of Rusts in which the life-cycle has been reduced by the dropping out of a variable number of the spore types. These are known as **short-cycle rusts.** The Hollyhock Rust, for example, only produces teleutospores and basidiospores, while the Antirrhinum Rust gives rise to uredospores as well. In all cases of short-cycle Rusts teleutospores are developed, from which the essential basidia can be formed. The cytological behaviour of these forms has not been fully studied.

It frequently happens that a heteroecious Rust may give rise to a short-cycle Rust when one of the two essential hosts is lacking. In South Africa and Australia, in the absence of the Barberry, a short-cycle form of *Puccinia graminis* is found in which only uredospores, teleutospores and basidiospores are produced, thus cutting out the part of the cycle involving the Barberry.

On the other hand, in America, and in particular in Minnesota, Dakota and Manitoba where the heteroecious form of *P. graminis* occurs, the Rust may cause a 50 per cent. reduction in the wheat crop, and rigorous methods are taken to eradicate the Barberry which is about as common there as the Bramble in this country.

A further complexity in the life-history of the Rusts is introduced by the existence of **biologic races.** Such races are morphologically indistinguishable from one another, but it is found that the spores of one race are usually incapable of infecting the host plant of another. Three important biologic races of *P. graminis* have been recognized, though a number of other less clearly defined races have been described.

Puccinia graminis tritici usually attacks Wheat only, though it may cause a feeble infection in Barley and Rye. *P. graminis avenae* attacks Oats, *Dactylis glomerata* and some other grasses, but not Wheat, while *P. graminis secalis* is found on Barley, Rye, *Agropyron repens* and some other grasses, but not on Wheat or Oats. It should be realized, however, that the series of biologic races observed in one country need not necessarily behave in the same way in another, and a biologic race which does not attack Wheat in America may be found to be a serious disease of Wheat in Australia or in this country.

Resistance to Wheat Rust has been studied extensively. It has been shown that susceptibility or resistance is dependent on one or more Mendelian factors (see Volume IV). By careful breeding and selection it has been found possible to produce a series of Wheats immune or largely resistant to Black Rust, though the process is a long one, for it does not of necessity follow that an immune variety is at the same time a good grower or a high-yielding strain. Work along these lines, however, would seem likely in the long run to produce more positive results than the wholesale destruction of Barberry bushes.

Ustilaginales

The Ustilaginales are Basidiomycetes in which the basidium is produced from a chlamydospore. It is either transversely septate and bears the basidiospores laterally, or unicellular and bears the basidiospores terminally. The **chlamydospores** are thick-walled, spherical spores which are formed as swellings of the hyphae within the tissues of the host.

The Ustilaginales include the Smuts or Brands and constitute important diseases of cereals. They live as obligate parasites, and infection takes place usually either through the flowers or at a very early stage of the seedling. In some genera asexual conidia are also formed.

Compared with the Urediniales the Smuts have a simple life-cycle. They have as a rule only two types of spores, the chlamydospores and the basidiospores. The latter have been shown to be of (+) and (−) strains, and chlamydospores are only produced, and the life-cycle completed, after a union of mycelia of (+) and (−) strains. They must therefore be classed as heterothallic.

We shall consider the genus *Ustilago*, but rather than select a single type species it is preferable to consider together the five species which are important diseases of economic cereal crops.

Ustilago (Smuts of Cereals)

The crops attacked are Oats, Barley and Wheat, all of which when affected by these parasites show certain obvious and very similar characteristics. From flowering time onwards some of the ears appear blackened and shrivelled, the grain being replaced by a loose, dark-brown powder which is composed of the chlamydospores of the Fungus (Fig. 301). Despite the fact that infection actually occurs at an early stage in the development of the grass it does not make its visible appearance until the flowering stage, when it is seen that the whole tissue of the flower is abortive. Two types are recognized. The one which is called the Loose Smut develops a blackish powder which is exposed at flowering time and is blown away by the wind. The other is termed Covered Smut, and in this type the spores remain in the grain and are only liberated by the breaking of the wall of the grain which generally occurs during threshing.

FIG. 301.—*Ustilago avenae* attacking the flowers of Oats.

Actually five species of *Ustilago* are involved in attacking the three species of cereals mentioned, for Oats and Barley have both Loose and Covered Smuts, while Wheat is only attacked by a Loose Smut. The following table will make this clear :—

Type of Smut.	Oats.	Barley.	Wheat.
Loose smut . .	*Ustilago avenae*	*Ustilago nuda*	*Ustilago tritici*
Covered smut .	*Ustilago levis*	*Ustilago hordei*	...

So far as the spores are concerned there is little difference between them, but the species will only attack their own host plant, and the Loose Smut type will not produce the Covered Smut appearance or vice versa. On the other hand, artificial hybrids have been produced between the various spore types.

LIFE-HISTORY OF THE FUNGUS

The spores produced either in the flowers or in the grain are variously referred to as simply spores, brand spores or **chlamydospores** (Fig. 302).

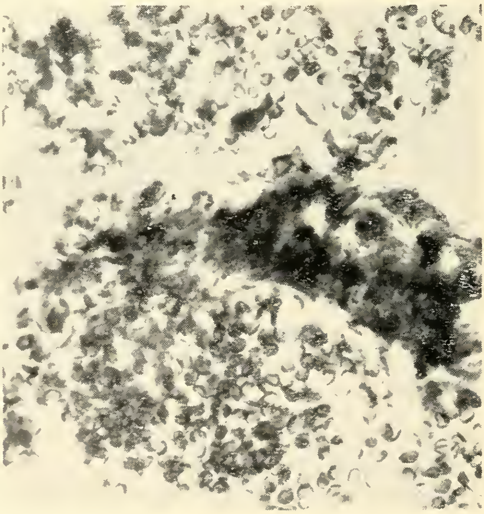

FIG. 302.—*Ustilago avenae.* Chlamydospores in the ovary of *Avena.*

They are black in colour and each spore has a fairly thick wall, which is slightly echinulate except in *U. levis* which is smooth. In the presence of warmth and moisture they germinate in about a day. The wall splits open and a short colourless hypha grows out. The nucleus of the spore divides twice, during which meiosis occurs, resulting in a row of four nuclei. This hypha functions as a **basidium,** and it becomes transversely septate into four uninucleate cells (Fig. 303). From the upper end of each cell a short **sterigma** is formed, from the outer tip of which a single **basidiospore** is abstricted.

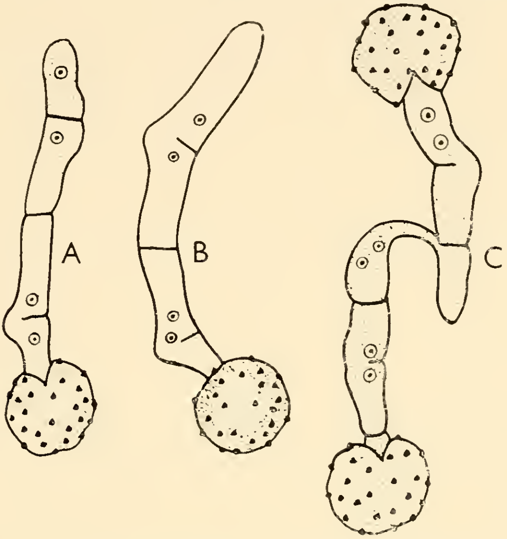

FIG. 303.—*Ustilago nuda.* A and B, Germination of chlamydospore to produce a four-celled basidium. C, Fusion of basidia from two chlamydospores. (*After Rawitscher.*)

The original nucleus of each cell divides into two, and one of the daughter nuclei then migrates through the sterigma into the basidiospore. These basidiospores are oval in shape and thin walled.

The segregation into (+) and (−) strains takes place during the meiosis before the formation of the basidiospores. As a result of cultural experiments in growing separately all four spores from a single basidium, it has been shown that segregation of the sexes may occur either in the first or in the second division. In an allied species *U. longissima*, for example, high temperature favours reduction at the first division. In another set of experiments it has been found that not only the temperature but also the Hydrogen ion concentration of the medium, as well as the concentration and relative proportions of Carbohydrate and Nitrogen in the medium are factors which determine whether the reduction shall be in the first or second nuclear division in the basidium.

These basidiospores may not immediately produce a hypha, but may develop by a process of yeast-like budding, whereby secondary spores are produced. This may occur particularly in manure heaps after smutted grain has been fed to stock.

These secondary spores are then capable of infecting fresh grain plants. It should be noted that the practice of spreading manure on fields shortly before cereal grain is sown means that these secondary spores are lying in a position entirely favourable for infection. In the case of Loose Smut, infection generally occurs only through the flowers, for the fungal mycelium cannot penetrate the tissues of the mature plants. On the other hand, the young seedlings can be infected up to the time when the first leaf is produced. Thus secondary spores lying in the soil may attack and infect young seedlings. In the case of Covered Smut the chlamydospores are already present in the grain, and if the grain is sown as seed a dormant mycelium may resume activity as the seed germinates and pass into the young shoot ; or infection may take place from outside through spores already liberated into the soil.

It is worthy of note that the chlamydospores, except in *U. avenae*, only retain their vitality for a few months, after which they cannot cause infection. Thus if the weather is wet at the flowering time of the cereal, most of the chlamydospores will be washed to the ground and the grain from that crop if used for seed will give rise to a new crop comparatively free from Smut.

Once penetration has occurred the mycelium makes its way to the growing apex of the plant and maintains its growth so as to keep pace with that of its host. These hyphae are intracellular and appear to cause little or no disturbance to the host plant. Hyphae in the older parts disappear, and it is only in the younger parts of the stem that active living hyphae can be found. When the flowers begin to form the mycelium enters the ovary where it forms a dense mass within the tissues, which are thereby destroyed.

After this has been completed the hyphal wall becomes gelatinous and swells up into segments which are then cut off by septa. These segments then give rise each to a single chlamydospore whose wall thickens and hardens as it separates from its neighbour, and the deep purple colour of the mature chlamydospore is assumed. Alternatively chlamydospores can be budded out laterally from the hyphae.

Little is known about the actual fusion of the mycelia produced from the basidiospores. Normally it would appear to take place within the host tissue, so that the cells of the resulting mycelium are binucleate as in the Rusts, union being effected during the maturation of the chlamydospores. Unfortunately the cytological details have not been critically worked out. In certain allied species, such as *U. violacea*, for example, the fusion has been observed. It may be brought about by the union of separate basidiospores which conjugate by means of a tube, through which the nucleus of one spore passes into the other (Fig. 303). Union may also occur between a basidiospore and a cell of the basidium. In either case the infecting mycelium is binucleate, and it is only from such a binucleate mycelium that chlamydospores can be developed. In *Ustilago*, therefore, the only uninucleate stage is the basidium.

Certain instances have been described in which there is union between basidiospores or mycelia of different species of Smuts. There is reason to believe that a natural hybrid between *U. avenae* and *U. levis* frequently occurs in nature. From experimental cultures it has been shown that such a hybrid assumes the appearance and mode of infection of *U. avenae*.

The life-cycle of *Ustilago* is represented by the following diagram (Fig. 304):—

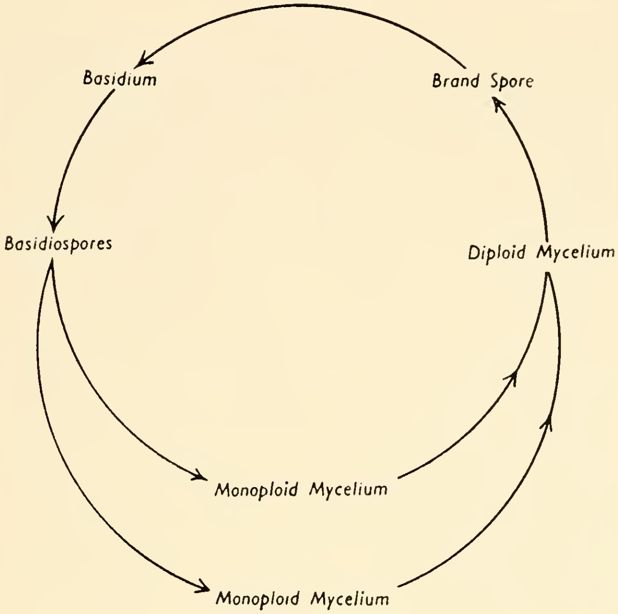

Fig. 304.—Life-cycle of *Ustilago*.

Importance of the Smuts to Agriculture

In former times losses due to Smuts not infrequently amounted to as much as 50 per cent. of the crop. The practice in modern times of dressing the seed with a solution of 1 fluid oz. of formalin to 2 gals. of water has reduced the loss to a very small percentage.

Particularly in America, Bunt or Stinking Smut, due to a closely allied genus, *Tilletia*, is probably a far more important disease. In this case the grains are invaded and the chlamydospores are liberated as in Covered Smut. The same formalin treatment is recommended in this case.

A number of **biologic races** of Smut Fungi have been described. It is not possible to go into the details here, but it is sufficient to point out that a strain which may cause a heavy grain loss in a particular variety of Oat may cause practically no infection in another. For example, a certain strain of *U. avenae* is found to cause high infection in the Oat variety called " Gothland," but seldom infects " Monarch," while, on the other hand, a certain strain of *U. levis* infects " Monarch " but not " Gothland." As a result of hybridization certain biologic races were obtained, some of which attacked one and some the other of the two Oat varieties mentioned.

Aphyllophorales

The Aphyllophorales are Basidiomycetes in which the basidia are undivided, but in which the hymenium is exposed from the first and spreads over the surface of either teeth, anastomosing gills or a smooth surface, or alternatively it may line, in the higher members, the inner surface of tubes.

The group is a large one containing many of the common Bracket Fungi which are so very characteristic of woodlands. It must be realized that these brackets are only the fruiting bodies borne on an invisible mycelium. This mycelium begins life either in the soil, from whence it gains entrance into the host through the roots, or it may enter the host tissue through a wound. The mycelium ramifies mainly in the phloem and the layers of thin-walled cells just below the bark, but some have the power of attacking lignin, so that they live not only at the expense of the elaborated food material produced by the host, but also upon the host tissue as well. In many instances, moreover, it is only when the life of the host tree is threatened, or in some cases when it is dead, that any fruiting body is formed at all. In fact prior to that time the presence of the Fungus may be quite unsuspected.

The fruiting bodies or **sporophores** are usually hard and woody in consistency, though in some species they may be more or less fleshy. They may develop rapidly and mature in a few months or they may be perennial, in which case a fresh hymenial layer is developed each year.

In addition to the normal fruiting bodies special fructifications of very variable form may be produced, particularly in the dark. Such fruiting bodies are often found developing on pit props. Though these bodies appear to be often sterile, it is said that sometimes they develop conidiospores. Conidiophores may also develop from the mycelium ; they are spherical bodies and each bears a cluster of oval or spherical conidiospores which germinate to produce a fresh mycelium. These conidiospores are stated to be diploid.

The mycelium, too, may form spores directly by the aggregation of the protoplasm into small areas, which then become surrounded by a wall. The spores so formed are usually spherical and thick walled. They are termed **oidia,** and are stated to be monoploid and to give rise only to monoploid mycelia.

Many of the species have been grown successfully on agar in pure culture. Under such circumstances it is often difficult to induce them to produce normal fruiting bodies, though some, after years of growth, do produce typical fructifications. It is not very surprising, therefore, that our knowledge of the developmental history of the various species is extremely scanty and no species has been adequately investigated. The following account of *Polyporus betulinus* serves to illustrate the more important features.

Polyporus betulinus (The Birch Polypore)

This species may be found growing very commonly in Birch woods, forming large fructifications on the trunks and larger branches of diseased trees. In badly infected woods it is not uncommon to find many of the trees in various stages of the disease. Firstly, there are trees in which the number of leaves and branches appears to be below the normal and in which many of the lower branches are dead. Secondly, there are those in which early stages of the fruiting bodies can be found and whose leaves have fallen by August. Thirdly, there are trees entirely defoliated and consisting of little more than gaunt, branchless trunks bearing fruiting bodies, and, finally, there are fallen trees on which the fruiting bodies may still be developing (Fig. 305).

FIG. 305.—*Polyporus betulinus.* Birch tree which has been killed by the Fungus, lying on the ground and bearing numerous fruiting bodies.

The mycelium develops just below the bark and forms a complete layer of tissue about the thickness of a piece of paper. It is white in colour and becomes more solid as the parasitism becomes more severe, until it forms a more or less complete investment of the central woody cylinder. It is made up of countless very fine, septate hyphae (Fig. 306).

We know little about the way in which the fruiting body is initiated, but it is apparently derived from this mycelium. It first appears as a more or less spherical knob of tissue which bursts through the bark. It may appear either on the main trunk or on the branches, but only boughs of considerable size normally bear fruiting bodies. They appear either high up or low down on the trunk and are not formed in acropetal succession but purely haphazardly.

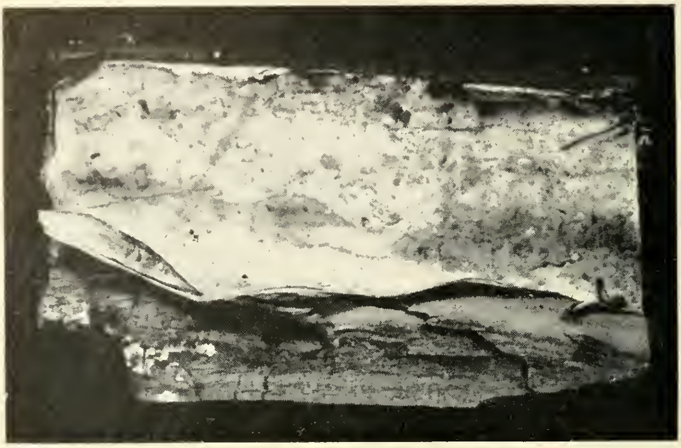

Fig. 306.—*Polyporus betulinus.* Birch bark covered with a papery tissue consisting of the Fungus mycelium which forms a layer between the bark and the wood.

This knob of tissue now enlarges and it is possible to recognize a very short stalk by which it is attached to the tree and a terminal rounded mass which is convex above and flat or slightly tilted to the horizontal below. The margin of the lower surface is much infolded (Fig. 307). As development continues the upper surface becomes flatter until finally it assumes a slightly undulating or completely smooth form. Meanwhile the margin has expanded and the lower surface has become flat and reniform or rounded in outline.

The lower surface remains smooth and flat, and is at first spongy, being covered by a fine downy layer of the mycelium. As development continues this layer becomes harder and minute holes appear in it, which are the beginnings of the pores of the hymenial tubes. These pores gradually increase in size by the drying up and dissolution of the covering membrane, until at maturity the pores appear as minute circular holes distributed over the entire lower surface of the fruiting body (Fig. 308).

A section through the sporophore shows it to be divisible into several distinct layers. The upper surface consists of a narrow zone of thick-walled hyphae which run parallel to the surface. These give off short branches, which terminate in oval cells and form a very fine roughening of the general surface. Below this the greater part of the body of the fructification is composed of very fine, anastomosing hyphae with large irregular spaces between them. This zone comprises about four-fifths of the thickness of the fructification. Towards the lower surface these anastomosing hyphae become more closely aggregated together and give off branches which turn and run down at right angles to the surface, to form the tissue of the tube walls (Fig. 309). At the lower surface these hyphae turn again and form the tissue over the pores, which in a young fruiting body consists of a continuous layer. As the tubes mature their openings are formed by the dissolution of these hyphae, so that in a section through a mature pore the margin is found to consist of an almost solid ring of disorganized cells which are slightly bent outwards to form a shallow collar or rim around the pore.

FIG. 307.—*Polyporus betulinus.* Fruiting body on the trunk of a Birch.

The **hymenium** which lines the tubes is formed from short branches

FIG. 308.—*Polyporus betulinus.* Fruiting body from the lower surface to show the very small pores.

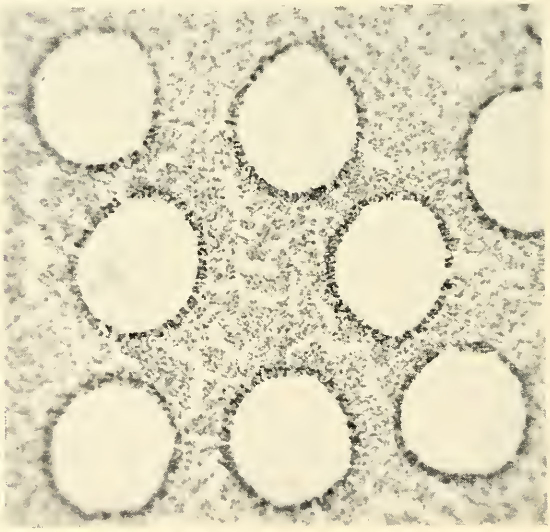

FIG. 309.—*Polyporus betulinus.* Transverse section through a portion of a fruiting body to show the pores lined with a hymenium forming basidia.

from the longitudinally running hyphae, which grow out and form a solid layer of cells at right angles to the length of the tube. It is from among these cells that the **basidia** grow out. They are somewhat larger than the sterile cells of the hymenium and project slightly into the cavity. Each basidium develops four short **sterigmata** from which four **basidiospores** are abstricted. These basidiospores are small and oval in shape. It appears that the continuous spore discharge, which is characteristic of these Bracket Fungi, is brought about partly by the upgrowth of fresh basidia from among those which have ceased to function and also by the progressive formation of basidia from the top of the tube downwards, as the thickness of the fruiting body increases and the tubes elongate. The period of spore discharge may continue for weeks or even months, and as a consequence the total number of spores discharged by a single fruiting body may run into millions.

Asexual reproduction by means of conidiospores occurs; these arise from the mycelium and may also be produced on the curious sterile fructifications, if any of these are actually produced by this species, but since the identity of these fructifications with any definite species is extremely obscure, we do not know whether they are ever produced by *P. betulinus*.

Polyporus betulinus has found certain technical uses. The fruiting bodies are employed at the present time in the manufacture of charcoal crayons, while formerly the surface of the upper tissue was found to make a very efficient razor strop.

Other Types of Bracket Fungi

In *Polyporus betulinus* the fruiting body only lasts for a single season, but in certain other types, for example, in the genus *Fomes*, the fruiting bodies are perennial. In such cases a completely new zone of tubes is formed below those of the previous year. These tubes may be almost continuous with those already existing, arising by the elongation of the longitudinally running hyphae of the tube walls, or in some species a zone of anastomosing hyphae may be formed first, from which the longitudinally running hyphae develop. Thus in a section of an old fruiting body of *Fomes applanatus* successive layers of tubes can be seen one below the other, resembling superficially the annual rings of growth of a stem. The age of such fruiting bodies therefore can be calculated by counting the number of successive tube layers.

In some species, e.g., *Polyporus dryadeus*, it appears that liquid is normally exuded from the tubes, and in these drops basidiospores occur (Fig. 310). Whether this exudation assists spore distribution or the germination of the spores is not known.

Many important plant diseases are caused by Fungi belonging to this large order, which contains several thousand species. Among those best known we may mention *Stereum purpureum*, which is the cause of the so-called Silver Leaf disease which is common on trees and most important when it attacks Plums. It first causes a silvering of the leaves due to the separation of the epidermis from the rest of the leaf tissue, which results in an air space being formed which reflects light. Later the branches begin to die back, and finally the whole tree dies.

Merulius lachrymans, the Fungus responsible for Dry Rot of timber is another member of this group. The fruiting bodies of the Fungus, instead of being produced in a bracket, lie flat or **resupinate** on the surface of the wood. Moreover, the hymenium is spread over the surface of very irregular, rather fleshy ridges somewhat resembling gills. The Fungus completely destroys the lignin of the wood it attacks. Species of *Fomes* are also responsible for the destruction of timber, either in the living state or after seasoning.

FIG. 310.—*Polyporus dryadeus.* Two fruiting bodies developed on Apple showing the exudation of moisture from the pore surface.

Fomes annosus, which attacks Pines, lives first as a parasite and later as a saprophyte on the dead trees.

Several species are used economically ; some are employed as food, e.g., *Fistulina hepatica* (Beef Steak Fungus), which forms large fleshy brackets on Oaks. *Fomes officinalis* was used medicinally because of the quinine-like taste which it possesses. *Fomes igniarius* was once used to prepare high quality tinder.

Agaricales

The Agaricales are Basidiomycetes in which the basidia are arranged over the surface of plates of tissue called **gills.** These gills are borne radially, arranged on the under surface of the fruiting bodies which generally consist of a stalk and a cap.

It is to this group that the mushrooms and toadstools belong. Many occur on the ground, some are produced on dead or decaying wood, whilst a few live parasitically on trees. Many of them form what is known as a **mycorrhizal association** with flowering plants among which they live. We shall consider later on (see Volume IV) the details of this association. It is sufficient for us to note at this stage that many toadstools can live only in association with particular plants, especially trees, and it is for this reason that we frequently find certain kinds of toadstools restricted to certain types of woodlands. For example, the common Fly Agaric forms a mycorrhizal association with the roots of the common Birch, and it is for this reason that this particular toadstool is most commonly found in a Birch wood. In some instances this association between the Fungus and the higher plant leads to the formation of what are called **Fairy Rings.** These are particularly noticeable on sheep-cropped grassland, where we find a difference in the colour of the grass closely associated with a ring of fruiting bodies. Not all Fairy Rings show these changes in the colour of the grass, since the association between the Fungus and the host varies. At least three distinct types of Fairy Rings are recognized. The explanation of such a ring is interesting, in bringing out the relation between the Fungus and the grass (Fig. 311). On germination of the spore a mycelium develops, which radiates out equally in all directions. The hyphae attack the roots of the grass,

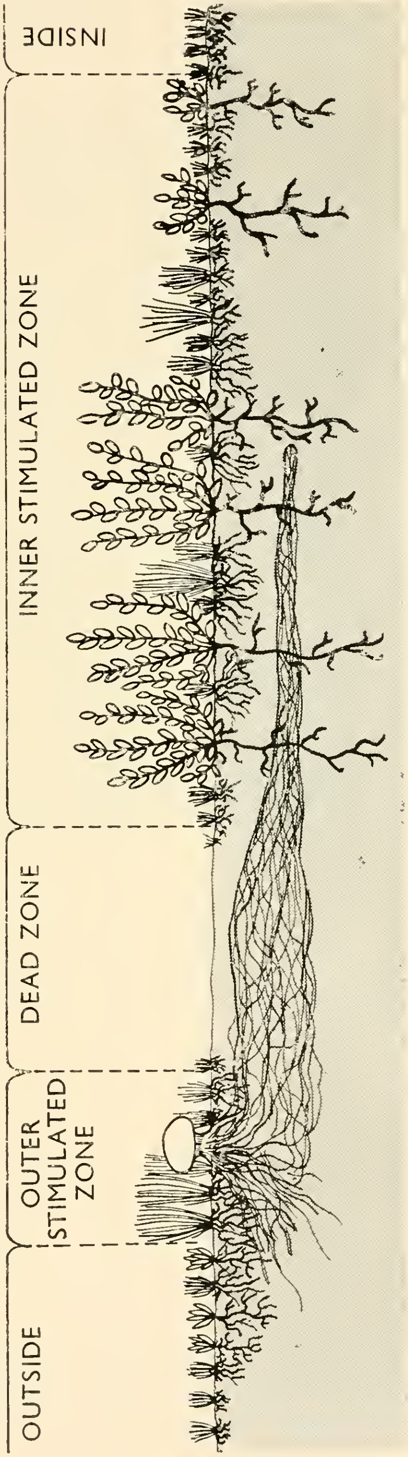

Fig. 311.—*Psalliota tabularis.* Diagram of section from the centre to the circumference of a Fairy Ring, showing relation between the mycelium and the growth of higher plants. (*After Buller.*)

which during the first year are stimulated by the union, and this is marked by a darker and more vigorous zone of grass plants ; subsequently in the second year, as the Fungus gains the upper hand, the roots are killed and the grass dies. Later, in the third year, after the fungal mycelium has migrated farther out, the grass recovers and regains its normal colour, growing more vigorously on the humus left behind by the dead zone of grass. In the autumn, or in some species, in the spring, the fruiting bodies of the Fungus are developed near the extremities of the mycelium's growth.

FIG. 312.—*Marasmius oreades.* Fairy Ring in grass.
(*From a photograph by H. Bastin.*)

We may therefore regard the ring of fruiting bodies so produced as an indication of the size of the Fairy Ring, and it will be found that this coincides approximately with the well-marked darker grass ring which we can see (Fig. 312).

As our example of this group we shall consider the Common Mushroom, formerly known under the name of *Agaricus campestris*, but more correctly *Psalliota campestris*.

Psalliota campestris (The Common Mushroom)

The Mushroom grows chiefly in meadows, where its mycelium feeds either on the roots of grasses or on manure and humus deposited in the soil (Fig. 313).

The **mycelium** consists of masses of **hyphae**, frequently twisted together into thick cords or **rhizomorphs,** which in their early stage are made up of uninucleated cells. Later, two hyphae come into contact and fuse, and a nucleus from one hypha passes into the nearest cell of the other hypha.

This only occurs when hyphae of (+) and (−) strains come into contact. A **clamp connection** is then formed (Fig. 314). In this process a small hook-like outgrowth is formed from the side of the cell. We will call the nucleus nearest to the hook A and that farthest off B. Nucleus A enters the hook, and both A and B divide simultaneously. The two daughter nuclei of B separate widely, one lying on each side of the place where the hook has formed. One daughter nucleus of A moves back into the cell and then two contiguous cross walls are formed, one cutting off the hook from the cell, the other cutting the parent cell in half. Lastly, the tip of the hook fuses to the hypha and the other daughter nucleus of A moves into the cell to join the daughter nucleus of B. The result is two cells, each containing one daughter nucleus from both A and B. The hook remains as a permanent attachment of the hypha. Every subsequent division is carried out in the same way. The possession of clamp-connections is therefore a mark of a binucleate mycelium.

Fig. 313.—*Psalliota campestris.* Mature fruiting body taken to show the annulus and the gills bearing dark spores.

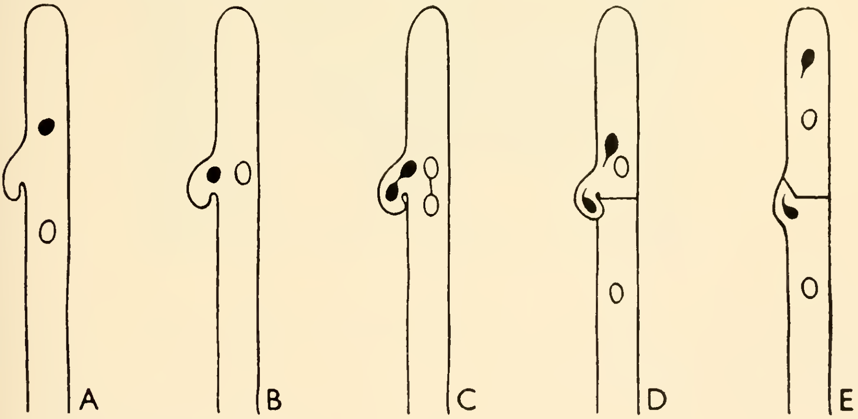

Fig. 314.—Diagram of clamp connections. A to E, Successive stages in the process. For details see text.

The mycelium remains binucleate until fruiting bodies or **sporophores** are formed, which, so far as is known, can only develop on a mycelium of this type. During the development of the fruiting body some of the cells become multinucleate, though the basidia are binucleate.

Development of the Sporophore

The fruiting body of the mushroom arises as a tiny knot of hyphae, which become aggregated together on the subterranean mycelium. It assumes a more or less elliptical shape and, at an early stage, a rudimentary ring-shaped channel appears around that part which will eventually produce the stalk. This channel develops into a hollow which will later form the **gill cavity** (Fig. 315). From the roof tissue of this cavity, which will eventually form the cap, slender, pointed, downwardly growing hyphae push into the gill cavity and form the **gills,** while the cavity itself enlarges in size. These gills form a series of radiating plates.

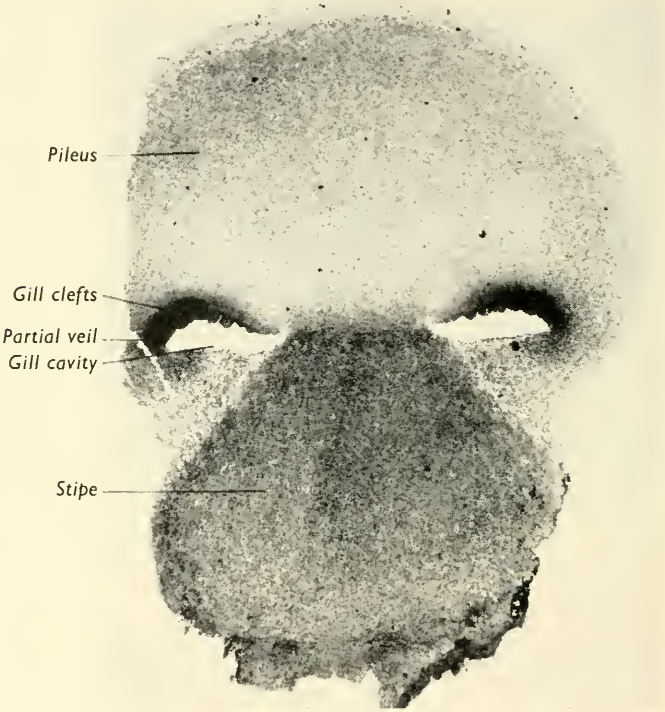

Fig. 315.—*Psalliota campestris.* Vertical section through a young fruiting body showing the development of the gill cavity.

At an early stage the cap is enveloped in a loose-meshed tissue which extends downwards to the stem. The extent of this tissue varies in different genera. In some, like *Amanita*, it may extend right over the whole of the cap and stalk forming a **universal veil,** but in *Psalliota* and in a number of other genera the veil extends only into the stalk below the gills and is termed a **partial veil.** In many other genera no veil is formed and the gill cavity is, from the first, exposed to the exterior.

As the gills develop the stalk or **stipe** begins to elongate, particularly in the region of the gill cavity, bursting the veil and carrying up the cap or **pileus** on its top. The veil, thus broken, remains partly as a vestigial structure on the top of the pileus and partly as a ragged fringe of tissue attached to the stipe, called the **annulus.** In the case of *Amanita*, the universal veil is ruptured in two places, one above and the other below the annulus so that a cup-shaped **volva** is left around the base of the stipe.

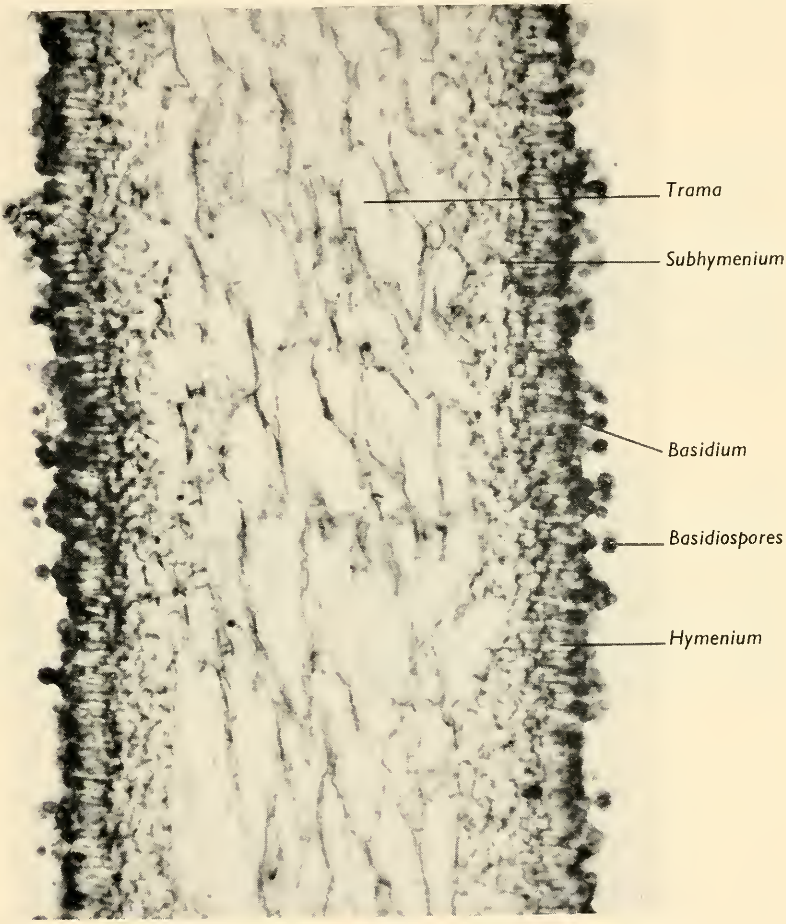

FIG. 316.—*Psalliota campestris.* Section through a portion of a gill to show the hymenial layer and the basidia with basidiospores.

In the mature fruiting body of *Psalliota* the gills radiate out as a series of flat, thin plates which are not joined to the stipe, though in other genera they may not only join but run for some distance down it. These gills exhibit a complex structure (Fig. 316). There is a central core of tissue or **trama,** composed of anastomosing, irregularly interwoven hyphae which give off short branches running obliquely outwards and forming a more compact tissue known as the **subhymenium.** From this layer the **hymenium** arises, which is composed of **basidia** and **paraphyses** arranged side by side. The basidia are club-shaped cells which are at first binucleate, but as they mature the nuclei fuse. It will be seen that the two nuclei which first come together at the union of the (+) and (–) mycelia finally unite in the basidium. The paraphyses are similar in shape to the basidia, but there is no nuclear fusion in them.

After fusion the nucleus in the basidium undergoes a meiosis, resulting in the formation of four monoploid nuclei (Fig. 317). At the end of the second division **centrosomes** * attach themselves to the wall at points which become the positions of origin of the **sterigmata.** These four sterigmata are narrow tubes from the ends of which the **basidiospores** develop, and into each of which one monoploid nucleus enters. This migration of the nucleus is apparently effected by the initial migration of the centrosome, which leaves behind a stainable thread, possibly analogous to an astral ray, which draws the nucleus through the narrow sterigma into the spore. Meanwhile the basidium becomes vacuolate and the pressure produced by this may not only cause the flow of the nucleus and cytoplasm into the spore, but may also assist in the final discharge of the latter.

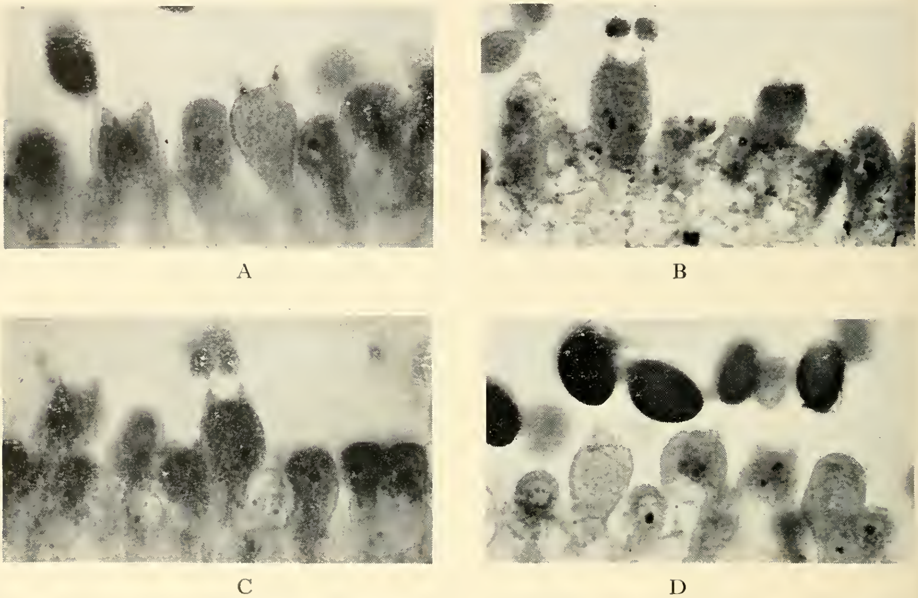

Fig. 317.—*Psalliota campestris*. Cytology of the basidium. A, Formation of sterigmata and migration of nuclei into them. Nuclear divisions can be seen in some basidia. B and C, Development of young basidiospores. D, Mature basidiospores. A second division appears to be in progress in the basidium which may give rise to a second crop of spores.

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* Centrosomes are minute granules commonly associated with the nucleus in animal cells and found also in some of the lower plants. They form the points of origin of the spindle fibres during mitosis.

SPORE DISCHARGE

The four spores on a basidium are not all shed together, but successively, a few seconds or minutes after one another. A few seconds before the spore is actually shed a drop of liquid appears at the tip of the sterigma. This drop has a diameter about half that of the spore and is shed with the spore. The spore therefore is very adhesive when first liberated. Each spore is shot off horizontally a distance of about $\frac{1}{250}$ in. (0·1 mm.), and it is probably the vacuolation of the basidium referred to above which provides the necessary force. The motion is at first more or less horizontal in the space between the gills, but, due to air resistance, this movement is soon brought to a stop and the spore begins to fall under the action of gravity. The fall is most rapid while the spore is still between the gills, but after about a minute it dries and the reduction in volume appears to reduce the rate of fall, which depends on the size and specific gravity of the spore. The rate of fall varies from $\frac{1}{80}$ to $\frac{1}{4}$ in. (0·3 to 6 mm.) per second (Fig. 318).

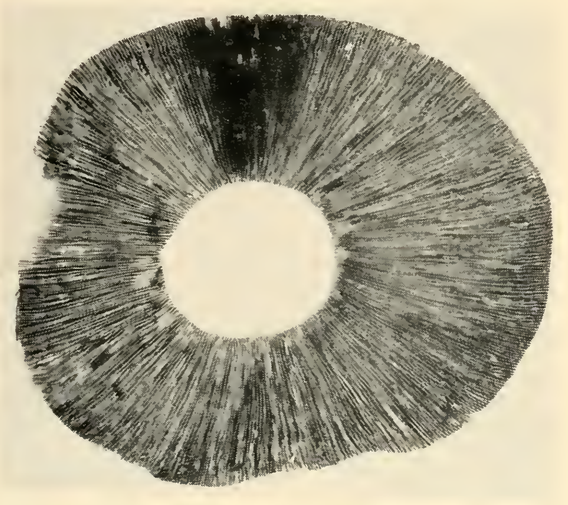


FIG. 318.—*Psalliota campestris.* Spore print on paper, deposited from a ripe pileus.

This peculiar method of spore discharge has an important bearing on the structure of the fruiting body. The violent expulsion ensures that the spore shall be shot clear of neighbouring basidia and will then fall freely between the gills, provided that they are vertical. A tilt of 2° 30″ out of the vertical is said to be sufficient to prevent some of the spores escaping, while at 5° half the spores will fall on the adjacent gill plates, and with a tilt of 9° 30″ four-fifths of the spores will fail to reach the exterior. These facts will explain why the fruiting body of a mushroom so rapidly orientates itself to the vertical if placed at an angle. Moreover it can be shown that it oscillates about the vertical before finally coming to rest. In some species in which the gills are rather close together we find that special thick cells, called **cystidia,** are formed on the hymenium which bridge across between the gills and may possibly help to keep the gills sufficiently far apart to allow the spores to fall freely.

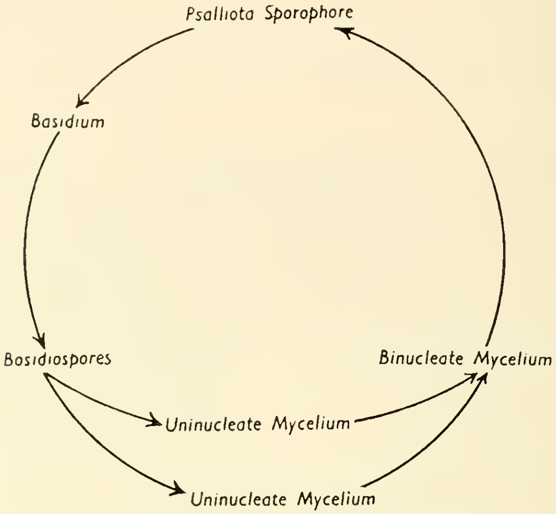


FIG. 319.—Life-cycle of *Psalliota campestris.*

SOME GENERAL REMARKS ON THE AGARICACEAE

In the cultivated mushroom only two basidiospores are produced on each basidium. This may be a degeneration as a result of cultivation, or may be the result of a mutation. In most instances the segregation of (+) and (–) strains takes place in the first division of the basidium, so that (+) and (–) basidiospores are produced in equal numbers. In certain species of the genus *Coprinus* the condition is more complex, for segregation appears to take place in the second division, so that four different types of spores are produced. Fruiting bodies are only formed when certain of these spore-types come together (see Volume III).

The genera of the Agaricaceae are separated mainly on the colour of the spores. In *Psalliota* they are purple, but white, pink, brown and black spores are found in other genera. Many of the species are edible, but several genera contain poisonous species, notably the genus *Amanita*, especially *Amanita phalloides*, the Vernal Toadstool, which is the most deadly (Fig. 320). This genus can be recognized easily by the white spores and by the fact that both annulus and volva are present, in contrast to the purple spores and no volva in *Psalliota*. It is important to remember, however, that the spore colour only develops after the stipe has begun to elongate, and that under certain conditions the volva may become almost completely fused with the base of the stalk. In the genus *Coprinus*, commonly known as the Lawyer's Wig, because of the shaggy exterior of the cap, the gills undergo a curious process of **autodigestion,** whereby the cap is digested from the edge upwards, while at the same time it becomes turned outwards (Fig. 321). This process may assist in the dissemination of the spores, for the gills are exceptionally long and are folded close around the stipe in such a way that only spores at the margin of the pileus could fall clear until by autodigestion the cap expands and exposes the upper part of the gills.

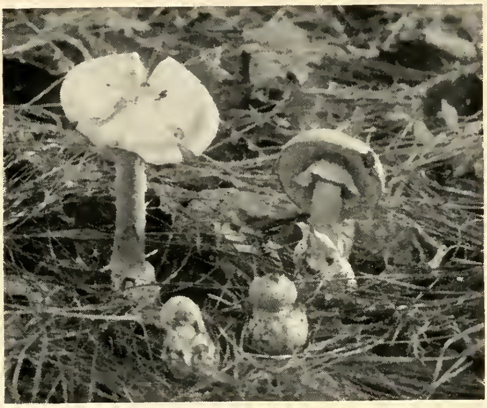
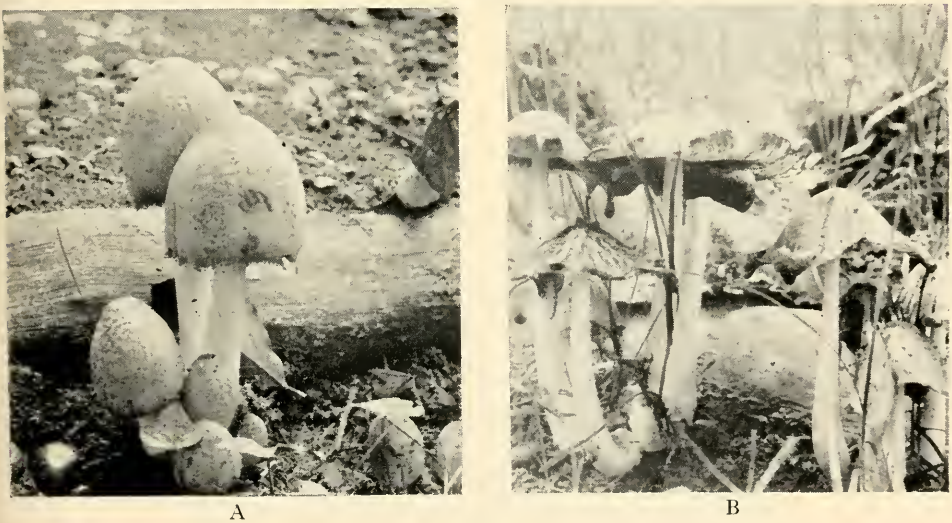


FIG. 320.—*Amanita phalloides.* Fruiting bodies in various stages showing annulus and volva. The gills bear white spores.



A

B

FIG. 321.—*Coprinus domesticus.* A, Young fruiting bodies. B, Fruiting bodies after the deliquescence of the gills due to autodigestion.

Spore production in many of the higher Fungi is enormous. It has been estimated that a mushroom about 3 in. across produces about 800,000,000 spores, while some of the Bracket Fungi and giant Puff Balls may produce from 11,000,000,000 to 7,000,000,000,000 spores. Bearing in mind that several fruiting bodies can be produced from one mycelium each year and that many mycelia are perennial, some idea will be gained of the scale of spore production. Nevertheless in a given area the population of any species is fairly constant, so that one realises the gross wastage of spores which must occur, and from a bionomic standpoint the reproductive mechanism in the higher Fungi appears to be very inefficient.

Before closing our account of the Agaricaceae we must refer to **luminosity.** Since classical times it has been known that decaying wood is sometimes luminous, for Aristotle and Pliny refer to it. It has been shown that the mycelium of many Fungi is capable of producing light, sometimes in sufficient quantity to be visible for 20 yds. This luminosity can only appear in the presence of oxygen and is probably due to chemical changes of a doubtful nature. It appears to have no biological significance. One of the more striking examples is seen in the rhizomorphs of the Honey Fungus, *Armillaria mellea,* which is a very important wood-destroying Fungus in this country. These rhizomorphs form an almost complete mat of tissue in the region of the phloem of the host plant, and if the bark is stripped off the light emitted by the hyphae is sometimes clearly visible at night.

Gasteromycetes

The Gasteromycetes are Fungi in which the hymenial surface is enclosed in a **peridium.** The interior of the peridium is composed of a chambered tissue called the **gleba,** on the surfaces of which the hymenium develops. In this way spores when mature are shed into the chambers, and as more and more spores are developed the whole interior of the peridium becomes filled with spores, while the gleba gradually disorganizes and dries up after the formation of the spores.

Fig. 322.—*Lycoperdon pyriforme.* Cluster of fruiting bodies at the base of a tree stump.

Typical examples of the Gasteromycetes are the Puff Balls and Earth Stars belonging to the genera *Lycoperdon* and *Geaster* respectively.

In the genus *Lycoperdon* the peridium may become thin and dry when mature. A perforation opens in the top of the peridium and the spores are scattered by the wind (Fig. 322). In the genus *Geaster* the peridium splits into an outer layer which folds back like the rays of a star, exposing an inner sac containing the spores, which opens as in *Lycoperdon* (Figs. 323 and 324).

FIG. 323.—*Geaster triplex*. Group of fruiting bodies developed on the ground among Beech leaves.

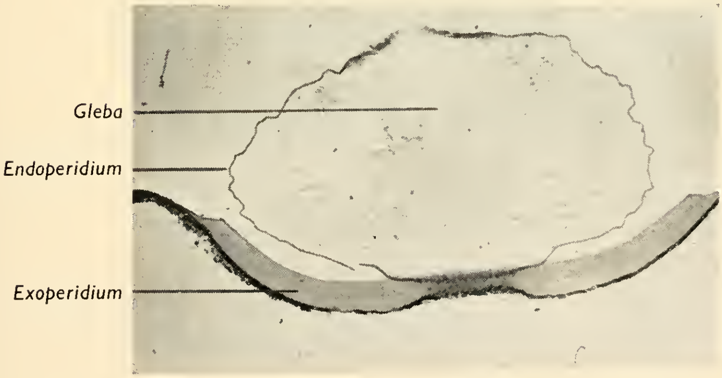


FIG. 324.—*Geaster triplex*. Vertical section through a fruiting body to show the various parts.

Some of these Puff Balls reach a considerable size, and the giant Puff Ball (*Lycoperdon giganteum*) may measure as much as 3 ft. across. It is found on grass, and not infrequently appears on golf courses. Even more remarkable are certain genera which live exclusively below ground. Little is known about them, but it has been suggested that the spores may be distributed by earthworms.

Few Gasteromycetes have been critically studied, and we shall confine our attention to two fairly well-known types, *Cyathus striatus* and *Phallus impudicus*.

Cyathus striatus

This very beautiful little Gasteromycete is found growing fairly commonly on stumps or on the ground among dead leaves in woods. In shape it resembles an inverted bell, the outside of which is reddish brown in colour and distinctly hairy. The interior is lead coloured, fluted and smooth. In the young state the bell is covered by a thin pale membrane, the **epiphragm,** but this soon disappears exposing a number of whitish, sub-circular bodies, the **peridiola,** which are attached to the inner wall by a short cord or **funiculus.** The whole fruiting body is about 1·5 cm. high, but as it is usually produced in groups it is relatively easily recognized (Fig. 325).

FIG. 325.—*Cyathus striatus.* Group of fruiting bodies developed on decaying wood among leaves.

On account of their peculiar appearance this and two allied genera, *Crucibulum* and *Nidularia*, are collectively spoken of as the Bird's Nest Fungi.

DEVELOPMENT OF THE FRUITING BODY

The mycelium is composed of binucleated cells, and clamp connections are formed abundantly. With the inception of a fruiting body certain hyphae become matted together into a small whitish knot. At the base of the knot the hyphae grow out in a fan-like manner and surround the knot itself. Meanwhile from the knot is differentiated internally a mass of very fine, much-branched and intricately interwoven threads. Later this mass separates into a closely woven lower part and a less dense upper part with large spaces between the hyphae.

Gelatinization now commences, beginning just below the interhyphal spaces and spreading down towards the base of the knot in an inverted dome. The tissue in the inside of this zone is formed of small-celled filaments from which the **gleba** becomes developed, while the outer tissues constitute the **peridium.**

As growth continues the peridium becomes differentiated into three layers. The outer layer or **exoperidium** is made up of loosely interwoven, longitudinally running filaments which give rise externally to numerous septate hairs. The inner layer or **endoperidium** is broad and is composed of gelatinized filaments which extend inwards to the gleba. Between these two layers there is a **middle zone** consisting of a pseudoparenchyma. It should be noted that it is partly on the structure of the peridium that the genera of the Nidulariaceae are separated. In *Nidularia* the peridium consists of a single layer, in *Crucibulum* there are two layers, the exoperidium and the endoperidium, while in *Cyathus* a third layer is differentiated.

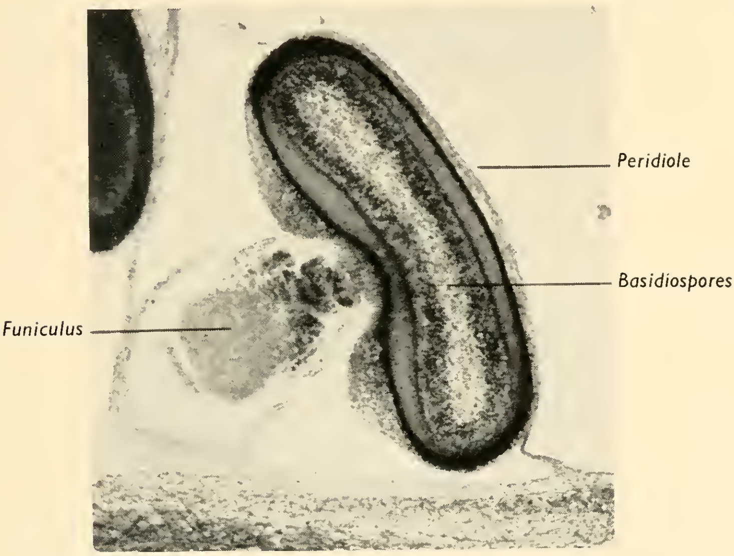


Fig. 326.—*Cyathus striatus.* Vertical section through a peridiole to show the internal cavity lined with basidia and the stalk by which the peridiole is attached to the wall of the fruiting body.

While the development of the peridium continues, the gleba also undergoes differentiation, and circular areas are formed composed of zones of densely interwoven hyphae, each of which later forms a separate, flattened, plate-like body, the **peridiole** (Fig. 326). As growth continues the peridiole enlarges and a space appears at the centre which is at first filled with a gelatinous material, probably produced by the dissolution of the central hyphae. This internal cavity gradually assumes an oval shape, enlarges, and is finally lined by a definite palisade layer composed of hyphae with swollen ends. Some of these cells are at first binucleate, but when the peridioles are mature the nuclei of these cells fuse to form the primary nuclei of **basidia,** which are thus separated from one another by uninucleated **paraphyses.** From these basidia the **basidiospores** are abstricted into the central cavity of the peridiole, which in this way become filled with basidiospores which are said to be binucleate.

During the internal development of the peridiole its external tissue becomes differentiated into a thin, colourless, easily removable coat covering a pseudoparenchymatous inner layer, so that at maturity a number of separate layers can be made out between the hymenial surface and the outer surface of the peridiole.

In *Cyathus striatus*, as in other members of the genus, the peridioles are attached to the endoperidium by means of a short cord or **funiculus** (Fig. 327). This consists of a spirally twisted mass of longitudinally running

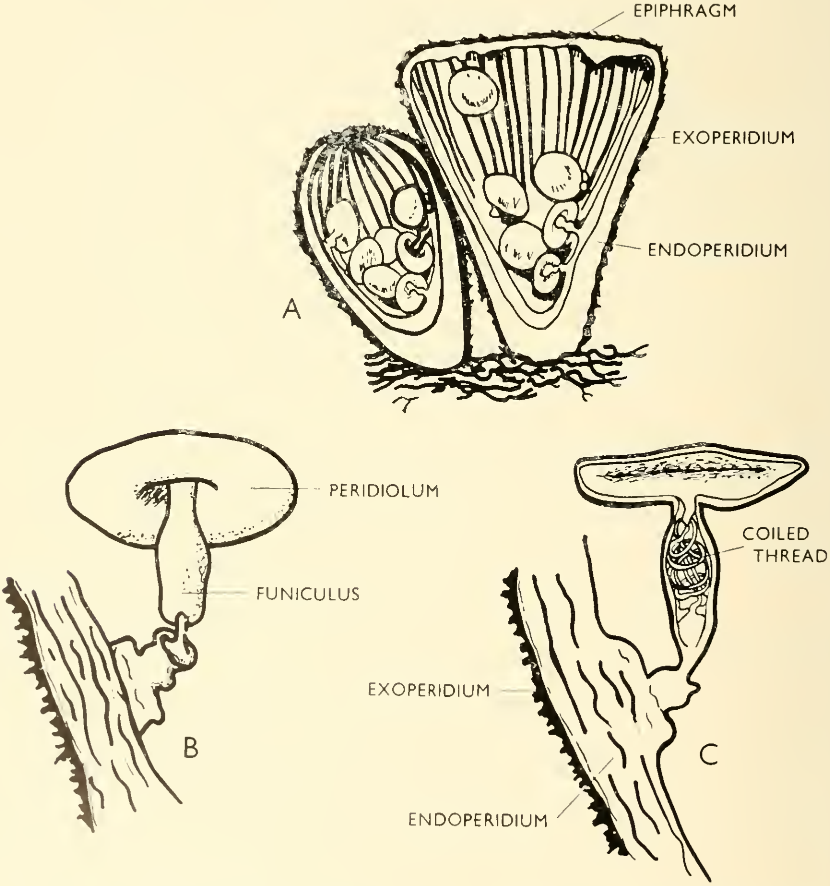


Fig. 327.—*Cyathus striatus*. A, Vertical section through two fruiting bodies showing on the left the young closed state, and on the right the fruit opened and the epiphragm ruptured. B, A peridiolum. C, Section showing the coiled thread in the stalk of the peridiolum and its attachment to the endoperidium. (*After W. Smith.*)

hyphae, which are attached to the centre of each peridiole by a small nipple-shaped mass. When this funiculus is mature it is usually quite short. The hyphae, however, are surrounded by mucilage, and when moistened they swell and the whole thread becomes softened, so that it can be pulled out to a length of 3 or 4 cm. Nothing is known of the function of this expanding thread, though it has been suggested that it may assist in dispersal by animals.

As the development of the whole fruiting body proceeds lateral expansion takes place, and the upper part of the peridium becomes ruptured, leaving the inner tissues exposed. The gleba now undergoes gelatinization, beginning at the base of the fruiting body, and finally the peridioles are left lying freely in the central cavity of the fruiting body and covered only by an **epiphragm** across the top of the cup, derived from the surface layer of the gleba which has not gelatinized (see Frontispiece).

When the whole fruiting body is mature the epiphragm finally ruptures leaving the sporophore open at the top. The moisture resulting from the gelatinization of the gleba dries up and the peridioles sink to the bottom of the peridium whence they are finally scattered.

Phallus impudicus (The Stinkhorn)

This Fungus is well known in woods in this country where its presence may often be detected by its strong repulsive smell, before it can be seen. In the young state it appears as a mass of white gelatinous material, about the size and shape of a hen's egg (Fig. 328). Under conditions of sufficient water supply the fruiting body emerges from the egg with surprising rapidity, taking about half an hour to grow to full size. When mature the fruiting body consists of a white basal cup or **volva,** derived from the wall of the egg, which has burst to liberate through its top a long, thick, but very spongy **stipe** or stalk. On the top of this is borne a small conical cap or **pileus,** whose outer surface is convoluted or thrown into shallow folds and is covered by a **gleba,** consisting largely of greenish, gelatinous material and of **basidiospores.** It is this greenish slime which gives off the nauseating odour which attracts flies, who eat the sweet slime and at the same time the basidiospores. In fact it has been proved that the basidiospores germinate better after passage through the alimentary canal of a fly than otherwise. These basidiospores on germination give rise to a fresh mycelium from which a fresh fruiting body arises. No details of the cytology have yet been studied, and it is not known whether a union of two monoploid mycelia is necessary before the fruiting body can be formed.

Development of the Sporophore

The details of this process are elaborate, and it is difficult to indicate any homology between the structures in *Phallus* and those in other Basidiomycetes.

Before a fruiting body is initiated the hyphae of the mycelium become aggregated together into thick strands or **rhizomorphs,** which may be traced for considerable distances from the fructification. The latter structure begins as a little ball of hyphae at the end of a rhizomorph. In this two zones are differentiated, an outer rind, the **exoperidium,** which is continuous with the cortex of the rhizomorph, and a central portion, the **columella,** which is continuous with the core of the rhizomorph. The tissue of the rind is very loose, and the hyphae at the head of the columella radiate out fanwise to make a sort of sheaf-like head, in which most of the development takes place. It expands greatly, and its outer layer gelatinizes and forms what is known as the **volva jelly,** which is conspicuous in the later stages of development. The inner portion forms an axial column, continued downwards into the columella, and a rather dense mantle around it (Fig. 329). This mantle, which forms a dome-like covering to the axial column differentiates again into a solid outer zone and a loose intermediate zone of radiating hyphae. The *inner* edge of the *outer* zone now produces a palisade layer of cells which becomes arched into irregular folds and pads, and this is the

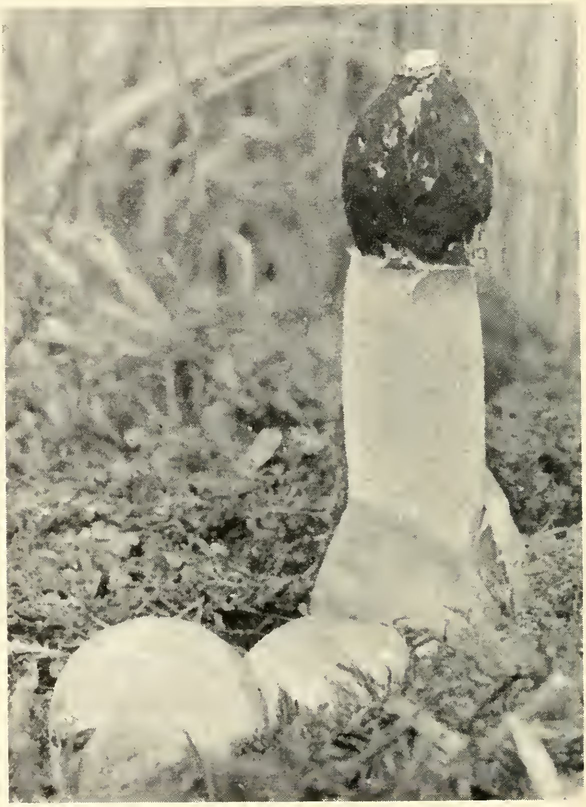


FIG. 328.—*Phallus impudicus.* Left, young fruiting body in the egg stage, and on right a mature fruiting body with exposed gleba.

beginning of the **gleba,** which bears the basidiospores. It is covered by a thin gelatinous **endoperidium.** The intermediate zone itself undergoes differentiation. It forms outwardly a dense layer, in contact with the glebal folds ; a thick middle zone, and, next to the columella, a close-fitting zone like a sleeve round the columella, which becomes first knotted and later spongy.

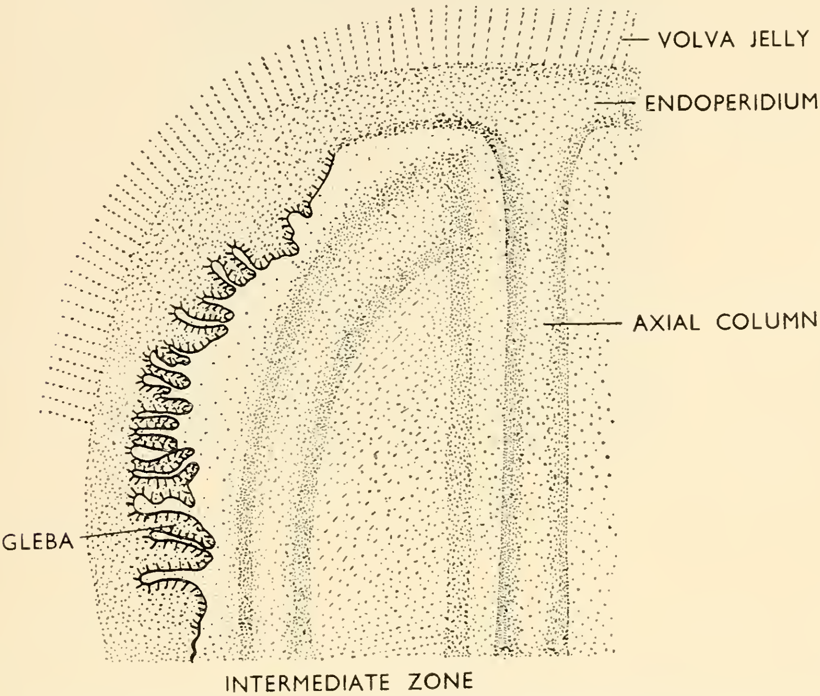


Fig. 329.—*Phallus impudicus.* Vertical section through part of a young fruiting body to show the various layers. (*After Fischer.*)

The outer dense zone and the thick middle zone contribute to building the **pileus,** which here forms a bell-shaped structure which lies beneath and within the dome-shaped gleba, instead of being outside and above the spore-bearing layer, as it is in the Agarics. By the time these structures have been formed the gleba has darkened to greenish-grey and has formed a thick layer of basidiospores, and its cells have broken down into a viscid mass. External to it is the layer of volva jelly and the exoperidium of the fructification, enclosing everything else in an " egg " (Fig. 330). The egg stage continues until all the inner tissues have matured.

Water is now absorbed and the axial column and the spongy sleeve around it become filled with water and expand. This ruptures the egg at the top, and the pileus and gleba are carried rapidly upwards on the expanding column, which is now known as the **stipe.** The exoperidium of the egg is left behind as a sheath at the base of the stipe and forms a **volva** corresponding to, or at least analogous with, that in *Amanita*. The viscid mass of the gleba is exposed on the pileus and is eaten and dispersed by flies.

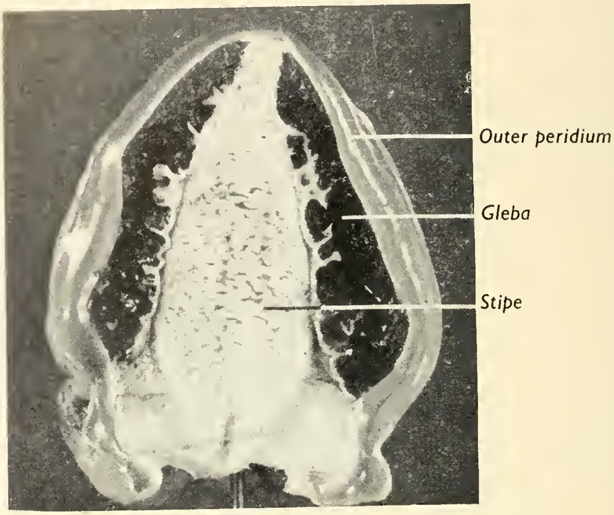


Fig. 330.—*Phallus impudicus*. Vertical section through an egg prior to the elongation of the stipe and the bursting of the outer peridium.

The Distribution of Fungi

Any consideration of the distribution of Fungi must necessarily take account of their mode of life, for, being either parasites or saprophytes, they are restricted in their distribution according either to the plants they live on or to the substrata upon which they feed. In general, we may say that the saprophytic forms are more widely distributed in nature than the parasitic species.

Comparatively recent investigations of the microflora of the soil have revealed many interesting points, though unfortunately insufficient work has been done upon the actual species inhabiting the soil in different localities to enable us to gain a very complete picture of distribution. Species of *Mucor*, for example, have been found to occur very commonly in the soil, and it now seems likely that the soil is the principal habitat for these Fungi. Some species, like *Mucor hiemalis*, are found equally commonly in all soils, while other species are limited to soils of a particular character. *M. ramannianus*, for example, occurs very widely in soils upon which Pine woods are growing. In Spruce woods, however, this species is replaced by *M. sylvaticus*.

The members of the Saprolegniaceae were until quite recently regarded as water Fungi, in fact they are usually referred to as the Water Moulds. It now appears probable that they are equally common in soils, and it may well be that those species found in water have actually come to live there because the zoospores were washed out of soil by rain.

Many studies have been made of the Fungi which occur on dung, and a whole volume might be written upon the dung flora. If samples of dung are kept moist and warm a succession of Fungi will appear, and generally it is found that the same species occur on a sample of a particular dung and generally in the same order. First, various Mucoraceae make their appearance, to be followed by various small Pezizaceae, and later by certain Agaricaceae, particularly species of *Coprinus*.

Dead leaves, too, have their own characteristic fungal flora. Many of them are soil Fungi, but some appear to have reached the leaves before they were shed. It is interesting to note in this connection that the number of species occuring on Oak leaves is much larger than those which occur on Beech; a point which may explain the relatively rapid decomposition of fallen Oak leaves as compared with those of the Beech.

When we turn to the distribution of the larger species, we find that other factors besides the Fungus itself play a part, for it has already been pointed out that the distribution of many of the Agaricaceae is determined by the mycorrhizal association between the mycelium of the Fungus and the roots of certain plants. In this respect many Fungi appear to be fairly promiscuous, while others are specific as regards their host plant. It follows, therefore, that the distribution of the higher Fungi is to a considerable extent dependent upon that of the phanerogamic vegetation with which they live. Later we shall discuss this question of plant distribution again in some detail, and it will suffice here for us to note a few general points about fungal distribution.

It has been found that the Fungus flora of woodlands fall into two distinct groups, that which inhabits deciduous woods and that which occurs in coniferous woodlands. For example, *Tricholoma virgatum* is common in Beech woods, while in coniferous woods it is replaced by *Tricholoma terreum*. Pastures and heaths also have their own Fungus flora, as any countryman knows who goes in search of the common mushroom. Even sand dunes have their own particular species, one, *Inocybe maritima* (Fig. 331), living in symbiotic association with the underground stems of the Marram Grass.

Certain Fungi choose particular localities in which to grow because of some mineral substance which they require. We have pointed out that *Pyronema confluens*, is mainly restricted to burnt ground, while it is recorded that after the disastrous earthquake and fire in Tokyo in 1923, within three days of the fire being put out large areas became covered by another similar Fungus, the orange-coloured *Neurospora sitophila*.

Many trees have their own particular flora of micro-fungi, quite apart from those species which are obligate parasites upon them, while other Fungi live exclusively upon one type of decaying material.

We will defer until Volume IV entering into the complex questions of the relationships which exist between parasitic Fungi and their hosts. Obviously they vary greatly in different cases. Some Fungi are widely distributed over a varied range of host plants, others are more limited in their preferences, while others exhibit biologic races which still further restrict the host range of the Fungus.

FIG. 331.—*Inocybe maritima.* Fruiting body of the Fungus, which generally occurs on sand dunes associated with *Ammophila arenaria.*

SPECIAL FEATURES OF FUNGAL NUTRITION

Fungi may be divided, as has been pointed out above, into saprophytes and parasites, but the latter group may also be divided into **obligate parasites** and **facultative parasites.** The former are incapable of growth on anything but a living host, and it is concluded that they require their food materials in highly elaborated forms, or, in other words, that they have little if any power of synthesis. The latter group of facultative parasites, however, are also able to grow as saprophytes on artificial media so that they must be able to build up their specific carbohydrates and proteins from relatively simple organic substances. Most can use simple sugars such as dextrose as sources of Carbon, and some can use even inorganic materials such as nitrates or ammonia as Nitrogen sources. The majority, however, require Nitrogen in organic combination, either as amides or amino-acids. The different powers displayed in this connection correspond no doubt to the presence or absence of certain necessary enzymes, since it is by means of specific enzymes that the nutrients obtainable are altered into assimilable forms and subsequently built up into the fungal substances, as well as into the numerous by-products of the metabolism. These are peculiarly numerous in Fungi and are often, as in the case of toxins, of great biological and economic importance.

The Ascomycete *Neurospora* has provided very interesting information about the synthesis of amino-acids. When ascospores of the Fungus are treated with X-rays or with ultra-violet light, then germinated and crossed with the opposite heterothallic strain, mutant forms are obtained which lack the synthetic ability to form certain amino-acids, due to the destruction of the controlling gene. By using mutants in which a particular stage in a synthesis is blocked, it has been possible to trace the course of some synthetic processes such as the formation of the essential amino-acid arginine from ornithine.

Fungi differ from the higher plants in some respects regarding inorganic nutrients. For example, the metals Calcium, Sodium, and Iron do not appear to be essential, though the anions phosphate and sulphate are necessary, as in green plants. The latter ion is sometimes absorbed in supra-optimal quantities (" luxury consumption ") and subsequently excreted. It has often been stated that certain of the heavy metals, such as Zinc, are essential to fungal growth, and that in this respect Fungi are peculiar, but recent work indicates that they do not differ significantly in this respect from the higher plants, many of which also require Zinc and other heavy metals. The fact is that the usual technique of cultivating Fungi on synthetic media revealed their nutritional demand for small quantities of certain elements, the so-called " trace elements," before the facts were appreciated in other groups. We now know that most, if not all, plants require for their complete nutrition a number of elements in extremely small amounts, among them being Boron, Manganese, Copper and Zinc. The absence of these elements is followed by depression or failure of growth. Fungi share this requirement. Thus the presence of Zinc in a culture medium favours sporulation and increases the dry-weight of mycelium formed, but it also increases the amount of sugar consumed per gram of dry-weight formed, or, in other words, the metabolic efficiency is lessened.

In addition to the inorganic trace elements Fungi require certain organic accessory substances or **nutrilites.** This was first observed by Wildiers in 1902 in the case of yeast, which he found required the presence of an unknown organic substance, derived from the yeast cells, which he called " bios." This is now known to be a complex of substances, among which the most important is Thiamin, usually called Vitamin B_1. This vitamin has been shown by Schopfer and others to be essential to the growth of many Fungi and beneficial in the majority of cases where it is not essential. These accessory substances are required in such minimal quantities that they cannot function as ordinary nutrients. Thiamin, for example, is active in amounts of no more than one part per billion of the culture fluid.

Fungi often produce excretory materials of a complex organic nature which affect the growth of others with which they are associated. The action may sometimes be stimulatory, as in the case of the bios substances, but is more often antagonistic or inhibitory, a condition which has been called **antibiosis.** The allied phenomenon of " staling " is usually attributed to an antagonistic action of the products either of one Fungus on its own growth or of the products of an associated species. Staling implies the depression or stoppage of growth, and it is due to the accumulation of staling substances of an excretory character in a limited quantity of growth medium, so that a toxic concentration is reached. It seems that such substances may be of quite simple character, and it has been shown that bicarbonates, and perhaps ammonia, are the factors chiefly influential.

The Origin of the Fungi

There are two possible ways in which the Fungi may have originated, and both receive some support in the light of modern knowledge. The older view was that the whole of the Fungi were derived from the Algae by loss of chlorophyll, and that the Fungi are nothing more than Algae which have become specialized to heterotrophic nutrition. As a result of parasitism, the rapid method of asexual reproduction has to a large extent replaced the more elaborate sexual method. Sexual reproduction, though still clearly seen in many of the less specialized types, has become progressively simplified until either only vestiges of a sexual apparatus remain or they have even completely disappeared. Supporters of this view point to the similarity of many Phycomycetes to Green Algae and of Ascomycetes to the Rhodophyceae. Even among the examples studied in this book we can see a distinct similarity between *Pythium* and *Vaucheria*, or between *Mucor* and *Spirogyra*. The female reproductive organ of *Aspergillus* is very similar to the carpogonium of *Batrachospermum*. The ascogenous hyphae of Ascomycetes may be compared to the gonimoblast filaments in the Rhodophyceae. Further, a study of the fungal components of certain Lichens emphasizes the remarkable similarity between the sexual reproductive organs of these Ascomycetes and of the Rhodophyceae.

It is not surprising, therefore, that the older mycologists considered the algal origin of the Fungi extremely possible, in fact in early times the Fungi were classified as non-chlorophyllous types following their supposed algal counterparts.

More recently, as a result of more careful study of the Fungi, this simple view has become less and less satisfactory. It has been pointed out that very few organisms exist at the present day which could be regarded as intermediate between Algae and Fungi, such as might be expected to occur if such a transition was still going on. *Polysiphonia fastigiata* is known to be a partial parasite on the Brown Wrack, *Ascophyllum nodosum*, that is to say, it grows more vigorously as a parasite than by itself, nevertheless it is still an obvious Alga. Two other red algal genera, *Harveyella* and *Choreocolax*, have gone further and have completely lost their chlorophyll ; they are still, however, typical Red Algae in structure, and no one would suggest that they resembled any known Fungus. Again the fungal cell wall is, with few exceptions, composed of completely different substances from those found in Algae. The storage of glycogen again is not an algal character, but is far more characteristic of animals. Heterothallism, at any rate in the higher

Fungi, cannot be compared with the sexuality in the Algae, and there are many other differences which might be detailed.

Whence then, we may ask, came the Fungi ? One modern view, which is steadily receiving more support from mycologists, is that they are a completely independent group, standing midway between the plants and animals and having no direct connection with either, except that at the dawn of evolution all life is believed to have had a common origin. In fact it has been suggested that the Fungi, or their ancestors, may have originated before either the plants or the animals. It is pointed out that in the absence of any form of life it would be possible for organic substances to have existed on the surface of the earth without undergoing decomposition, that is to say, organic substances derived from purely chemical reactions. On such food the first organisms could have lived as saprophytes.

From these saprophytic organisms, which may be regarded as the first Fungi, plants would be produced as a result of the evolution of a photocatalytic pigment which enabled them to synthesize their own food rather than rely upon material already elaborated. Parasitism then followed as the primitive saprophytic Fungi transferred their attention to plant life as a second means of obtaining food. In this connection we may note that even at the present time nearly all parasitic Fungi, however specialized, can fall back on a saprophytic existence if need be, as can be seen by their ability to grow on artificial media.

According to this view the animal kingdom was the last to be evolved, and again came from these saprophytic organisms, but here, instead of either making its own carbohydrates or living on the carbohydrates made by the plants, the animals devoured the plants and Fungi completely and thus a holozoic mode of nutrition became established.* It is interesting to note in this connection that there is at the present day a group of Fungi known as the Zoöpagaceae, which have adopted the habit of preying upon protozoal animals and Nematodes, which suggests that the hypothesis here outlined is not entirely fanciful.

If, then, the Fungi are really older in an evolutionary sense than either plants or animals, and if both kingdoms have originated from them, we should expect to find features exhibited which were characteristic both of animals and plants. This we certainly do. The simplest green plants are the Algae, the simplest animals the Protozoa. We have already indicated some of the points of similarity between Algae and Fungi ; analogous though not as clear comparisons are found with the Protozoa. We can clearly connect the plasmodium of the Myxomycetales with the Protozoa through the Rhizopoda ; in fact some zoologists consider that the Myxomycetales are animals and include them in the Protozoa as an order, the Mycetozoa. On the biochemical side the formation of glycogen, which is a distinctly animal substance, as a metabolic product in place of starch, is another strong link with the animal kingdom. On the other hand, true cellulose is formed

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* An alternative theory of the evolution of living organisms is referred to under Chemosynthetic Bacteria on p. 359.

by some Fungi, and this is essentially characteristic of plants, being very rare among animals. The cell walls of some Fungi do, however, contain chitin, which is again of animal nature.

If it is true that the Fungi have had an independent origin we must assume that all the types existing at the present time have been evolved from those primitive ancestral forms. We cannot consider this view in detail, but it is sufficient to say that no difficulty exists in tracing the main lines of such an evolution from the very simplest known Fungi to the more complex Phycomycetes such as *Mucor* or *Saprolegnia*. It is, moreover, quite possible to suggest ways in which the Ascomycetes may have arisen from a Phycomycete origin. In the opinion of those who support this view the similarity between the sexual apparatus of the Ascomycetes and the Red Algae is due to convergence, or the production of similar structures in response to similar environmental circumstances and requirements, rather than to any phylogenetic connection.

The Basidiomycetes stand apart in this consideration. Among all the forms known at the present day there is none which offers us any clue as to their origin. They show little or no connection with the Ascomycetes and comparatively little with the Phycomycetes. On the other hand, there is no group of Algae which can be pointed out as their possible ancestors. The fossil record tells us that in the course of geological time many families and even whole groups of organisms have died out, and it would seem that the types which gave rise to the Basidiomycetes may have completely disappeared. Whether they were Fungi or Algae it is fruitless to speculate.

CHAPTER VIII

THE BACTERIA AND VIRUSES

THERE is probably no group of organisms which has a closer association with man than the Bacteria. Owing to their ubiquitous occurrence he is brought into constant and unavoidable contact with them. They are to be found on all external parts of the human and animal body, and the respiratory and digestive passages contain a large and varied assemblage of forms, some of which are specially characteristic of these areas. Many of the diseases from which we suffer are brought about directly or indirectly through their influence, so that Bacteriology has become an important part of medical science.

Only a minority of Bacteria are harmful, however. The decomposition of organic substances which they bring about is essential to the normal circulation of nutrient materials, and it is not too much to say that but for their activities the continuance of life would be impossible. Man has also learned to take advantage of their chemical powers. He has utilized some fermentation processes from time immemorial, but in modern times Bacteria are being brought increasingly into use as agents in the manufacture of many industrial products, for which the rapidity and cheapness of their actions recommend them.

The real nature of Bacteria has only been understood comparatively recently, and even at the present time their structure is still obscure. This is chiefly due to their extremely small size, for they are the smallest of all living organisms. An average bacterial cell is only one twenty-thousandth of an inch ($1{\cdot}25\mu$) in diameter. There is considerable variation in this respect, the largest Bacteria ranging up to as much as 20μ in diameter, while the smallest are no more than $0{\cdot}1\mu$. Organisms of this order of minuteness can only be observed with the highest available magnifications, while the smallest lie at the extreme limit of microscopic visibility. Naturally their study therefore was impossible with the older forms of microscopes.

The relationships of the Bacteria are uncertain. The great majority are unicellular and possess no chlorophyll, their mode of nutrition being either parasitic or saprophytic. From this we might conclude that their nearest allies are the Fungi, but it is impossible to point to any group of the Fungi with which they show any relationships. Indeed in some ways they show a nearer approach to the Cyanophyceae among the Algae, which might have had a common ancestry with them. At present we can only regard them as a remarkably isolated group.

In spite of their small size it would be a mistake to assume that they are primitive organisms; on the contrary they are highly specialized to their mode of life and are so successful that they are man's most serious competitors. If we regard Man as the apex of that line of evolution which has stressed the development of relatively small numbers of large and complex individuals, we might also say that the Bacteria represent the extreme expression of the opposite trend towards the greatest possible numbers of the smallest individuals.

CELL STRUCTURE

Leeuwenhoek (Fig. 332), who discovered the Protozoa, was also the first to observe Bacteria, in 1683, but he thought they were animalcules, owing to their vigorous powers of locomotion. The movements of Bacteria are not entirely due to their own activity. Some are self-motile, but all alike show **Brownian movement,** which is purely physical and is exhibited by all small particles in suspension. This movement is caused by the bombardment of the particles by the vibrating molecules of the surrounding medium, which has no visible effect on large objects but sets up rapid oscillations in particles which are sufficiently small.

FIG. 332.—Portrait of Anton van Leeuwenhoek.
(*By courtesy of Dr. C. Dobell.*)

The **cell wall** is a rigid layer, apparently chiefly polysaccharide in nature, though fatty substances and proteins are also important constituents. True cellulose is of rare occurrence, but chitin is occasionally present. The outer wall is sometimes modified into a thick, mucilaginous **capsule,** as in the diplococcus of pneumonia. These capsules protect the enclosed organism against desiccation, and no doubt permit the dispersal through the air of the organisms which possess them.

Little is known as yet with certainty about the cell contents. The

cytoplasm differs from that of higher plants in its strong affinity for basic stains, in which it resembles chromatin. When this basophil cytoplasm is removed by acid hydrolysis, it is, however, possible to show that true chromatin occurs in granules, which divide when the cell divides and to which the term nucleus may be applied, though there is nothing like a fully organized nucleus (Fig. 333).

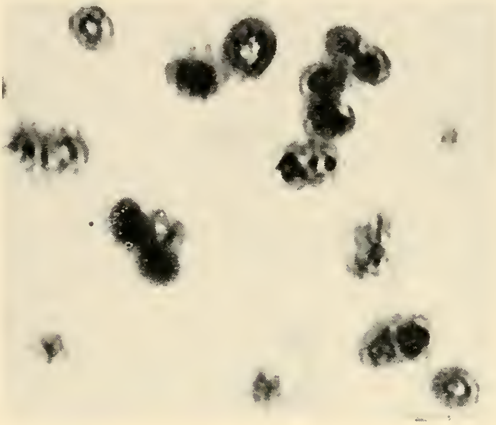

FIG. 333.—*Azotobacter chroococcum.* Stained to show nuclear bodies in cells.

Bacteria which are motile possess **flagella** (Fig. 334), filaments of extreme tenuity which are in some species attached all over the surface of the cell, and in others are confined to one or to both ends. Even in motile forms they are usually produced only by young cells and may be dropped off if multiplication becomes slow and the cells become senescent. They are presumably protoplasmic, as they show active gyratory movements and by their aid the cells can travel at surprising speeds. Instances are known of Bacteria moving 100 times their own length in one second, which is analogous to a speed of 400 miles per hour for man !

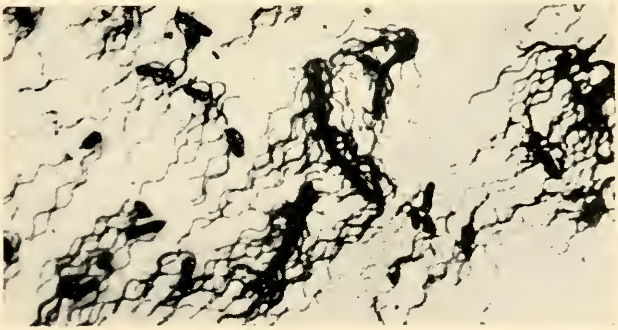

FIG. 334.—*Salmonella typhosa.* Stained to show flagella.
(*By courtesy of the General Biological Supply House Inc., Chicago.*)

Most Bacteria are colourless or only faintly coloured when seen in bulk, but some contain brightly coloured carotinoid pigments ; yellow, orange and red being the commonest tints. It has been suggested that these colours may serve as light filters, protecting the cells from the lethal effects of the shorter wave-lengths present in sunlight, to which the cells are sensitive. Most uncoloured forms are killed by even short exposure to sunlight, which has therefore a most important disinfecting influence.

A very interesting group, the Purple or Red Bacteria, which are common in natural waters, especially in the sea, possess two pigments, **bacteriopurpurin,** a porphyrin, and **bacteriochlorophyll,** which is related to chlorophyll. These pigments enable the organism to assimilate Carbon dioxide in the presence of light, with the liberation of Oxygen. They are unique in being the only organisms known to carry out photosynthesis without true chlorophyll.

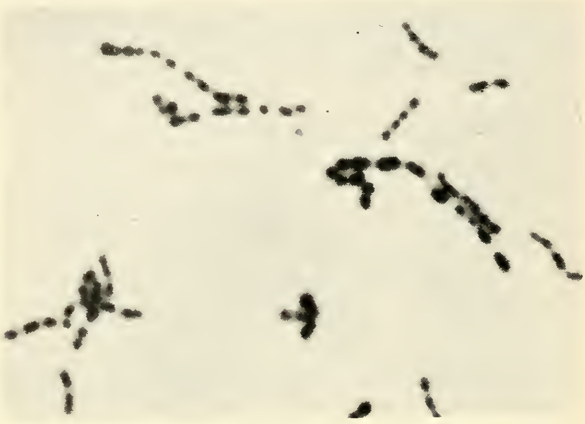

Fig. 335.—*Streptococcus salivarius.* Cells in chains. Gram stained.

Classification

Bacteria were classified in the past chiefly on their microscopical appearance, and many of the names thus given have been retained as the names of genera, although we now know that a true classification must take account of their biochemical properties as well as their structure.

The simplest form is that of a minute sphere, known as a **coccus.** When these occur separately they are put in the genus *Micrococcus* ; if in pairs they form the genus *Diplococcus* ; if in chains, the genus *Streptococcus* (Fig. 335) ; and, lastly, if in clusters, the genus *Staphylococcus* (Fig. 336). A peculiar type of aggregation is that into a cubical packet, which characterizes the genus *Sarcina*, one of the oldest names in Bacteriology, since *Sarcina ventriculi* was recognized in the human stomach as early as 1842.

Fig. 336.—*Staphylococcus aureus.* Cells in clusters. Gram stained.

Rod-like organisms are given the general name of **bacillus** (Fig. 337), though this name properly belongs only to one genus of the rod Bacteria. If the rod is curved it is placed in the genus *Vibrio*, or, if spirally twisted, in the genus *Spirillum.* Along with these are normally classed the **spirochaetes** (Fig. 338), with long, thin, wavy bodies, though their inclusion among Bacteria is questionable.

Fig. 337.—*Bacillus anthracis.* Mass of bacillary rods in kidney tubule of mouse. Gram stained. The causative organism of anthrax.

Bacteriology was for so long in the hands of men whose interests were primarily medical that the classification was unsatisfactory until an American

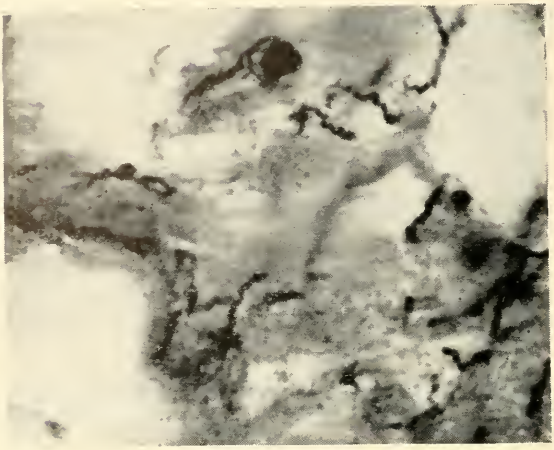

FIG. 338.—*Treponema pallidum.* The causative agent of syphilis. In liver of infected foetus. Silver stained.

committee was formed in 1917 to reduce it to order. In 1925 they recommended the following system, which has found wide acceptance, though it is still subject to modification.*

There are six Orders, containing the following principal Families :—

1. **Eubacteriales.**—The " True " Bacteria. Simple rods or cocci.
    - (1) Nitrobacteriaceae. Autotrophic Bacteria which carry out chemosynthesis (p. 359), *e.g.*, *Nitrobacter*, *Azotobacter*.
    - (2) Pseudomonadaceae. Rods with polar flagella, *e.g.*, *Pseudomonas*.
    - (3) Micrococcaceae. Spheroidal forms, not in chains, *e.g.*, *Staphylococcus*.
    - (4) Spirillaceae. Spiral rods, *e.g.*, *Spirillum*, *Vibrio*.
    - (5) Lactobacteriaceae. Acid producers, *e.g.*, *Lactobacillus*, *Streptococcus*.
    - (6) Parvobacteriaceae. Small parasitic rods, not active fermenters, *e.g.*, *Pasteurella*, *Haemophilus*.
    - (7) Enterobacteriaceae. Rods, mostly from the intestines. Active fermenters, *e.g.*, *Escherichia*, *Salmonella*.
    - (8) Bacillaceae. Spore forming rods. *Bacillus*, *Clostridium*.
2. **Actinomycetales.**—The " Ray Fungi." Thin filamentous forms which show a tendency to branching.
    - (1) Actinomycetaceae. Filaments long, branched and arranged in radial masses, *e.g.*, *Actinomyces*.
    - (2) Mycobacteriaceae. Filaments short, occasionally branched, *e.g.*, *Corynebacterium*, *Mycobacterium tuberculose*, the organism of tuberculosis.

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* Considerable changes in this classification were made in 1948, but it is still too early to say whether they will be permanent.

3. **Chlamydobacteriales.**—Cells arranged in chains with an investing sheath.
    Chlamydobacteriaceae. The only family, the so-called "Iron Bacteria," *e.g.*, *Cladothrix*.
4. **Thiobacteriales.**—The "Sulphur Bacteria." Form sulphur granules in the cells.
    (1) Rhodobacteriaceae. Purple Bacteria, *e.g.*, *Chromatium*.
    (2) Beggiatoaceae. Filamentous, no pigment, *e.g.*, *Beggiatoa*.
    (3) Achromatiaceae. Unicellular, no pigment, *e.g.*, *Thiophysa*.
5. **Myxobacteriales.**—Cells grouping themselves into variously shaped, macroscopic fruiting bodies, in which the rods become encysted in groups.
    Myxobacteriaceae. The only family, *e.g.*, *Myxococcus*, *Polyangium*.
6. **Spirochaetales.**—Thin flexuous filaments with terminal flagella or an undulating membrane attached along the body. Parasites.
    Spirochaetaceae. The only family, *e.g.*, *Treponema pallidum*, the causative organism of Syphilis.

Metabolism

It has long been realized that the microscopical appearance of these very simple organisms is insufficient to distinguish species from one another, so that the identity of a bacterium rests on its biochemical characteristics rather than on its morphology. These properties are not always constant, however, which has led to many difficulties, and the whole question of the constancy of bacterial species is still *sub judice*. Few things are more surprising than the extraordinary range of chemical reactions which can be displayed by the minutest and seemingly least differentiated of organisms. A single species, *Pseudomonas putida*, has been shown to assimilate as many as seventy-seven different substances as sources of Carbon. It is this chemical activity, in conjunction with their almost universal distribution in nature, which gives Bacteria their peculiar importance.

Among the most characteristic activities is fermentation, and it is upon tests of this power as applied to various sugars, polysaccharides, glucosides and alcohols that the discrimination of species is usually based. The organisms are grown in a culture fluid to which the fermentable substance and an indicator are added. A small inverted tube is immersed in the fluid to act as a gas-trap, and if fermentation occurs it is shown by the production of acid, with or without gas as well.

Bacteria vary widely in their power of synthesizing their food materials, and they may be divided into three classes in this respect.

1. Bacteria which can utilize ammonia as a source of Nitrogen and simple carboxylic acids as sources of Carbon. Some of the commonest soil organisms are in this group, *e.g.*, *Escherichia coli*

and *Pseudomonas fluorescens*. One member of this group can live on methylamine (CH_3NH_2) as its only organic material.

2. Bacteria which require amino-acids as a source of Nitrogen. This is a very large group, which vary widely in their demands. Among the amino-acids, tryptophane is the only one indispensable and is thus the only one which they cannot synthesize. In this group are *Bacillus subtilis*, *B. mycoides*, and the organisms of the " enteric " group, such as *Salmonella typhosa*.
3. Bacteria which have complex nutritional needs, including in many cases special " accessory " factors, such as vitamins. This group has the least power of synthesis and includes a few specialized parasites which will scarcely grow on artificial media. Here are included *Staphylococcus*, *Corynebacterium diphtheriae* and *Hemophilus influenzae*.

Most Bacteria utilize Oxygen for respiration, as do higher plants, and are thus **aerobes**, but Pasteur discovered that a number can dispense with it and that a few, known as **anaerobes,** cannot grow when Oxygen is present. Anaerobic respiration is closely allied to fermentation (see Volume III) and involves a linked reaction between an oxidizable substance which gives up Hydrogen and some easily reducible substance, which may be an organic substance or even a nitrate, to which the Hydrogen is transferred.

The yield of energy in this process of dehydrogenation is much less than in aerobic respiration, and the anaerobic organisms have remained on a lower plane of organization, but they are interesting biologically as their metabolism is more primitive than that of the aerobic organisms.

Reproduction

Bacteria form one of the very few groups of organisms which appear to be devoid of any sexual process. Observations have been made of cases in which the two halves of a dividing cell re-fuse with each other and this has been interpreted as a form of conjugation. Other and more doubtful observations suggest that in some cases large numbers of cells may become united into a free plasmatic mass, called a symplasm, from which new cells are segregated anew. Nothing in this connection is accepted as certain.

The universal method of multiplication is by **binary fission,** the cell dividing into two equal parts by a transverse constriction of the cytoplasm, followed by the deposition of a double cross-wall between the cells. The rate of division is dependent on the temperature, but at 37° C. it occurs, on the average, every half-hour. If every new cell formed divided again every thirty minutes the number produced would increase in geometrical progression. Thus one individual would produce in this way in twenty-four hours a total of 280 billion progeny, and if we assume that the volume of each cell is 25 cu.μ, the volume produced would be 7 litres of bacteria. This theoretical rate of multiplication can only, fortunately, be maintained for a short time and in the presence of unlimited food supplies. In practice the rapid consumption of the available food and the accumulation of injurious excretory products slows down the growth rate progressively until a stationary state is reached. When this occurs there is a rapid natural death, the number of survivors falling logarithmically, so that after seventy-two hours less than 1 per cent. of the organisms may be left alive. A few resistant individuals, however, may persist for weeks or even months.

Certain Bacteria, namely members of the family Bacillaceae, have the power of forming **spores** (Fig. 339), sometimes called **endospores** because they form inside the body of the organism and are liberated by its dissolution.

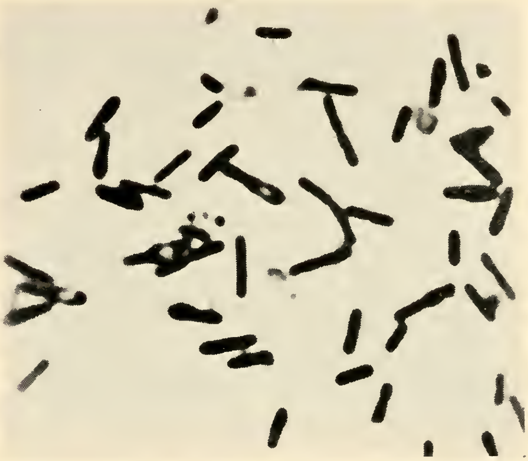

FIG. 339.—*Clostridium sporogenes.* Rods showing development of spores. Gram stained.

These spores possess an exceedingly impervious coat and show astonishing tenacity of life. They can withstand the action of many powerful killing agents, such as absolute alcohol or phenol, and they can remain alive for years in a dry state. They are also very resistant to extremes of temperature. Some, such as the spores of the anthrax bacillus, can withstand more than an hour's exposure to boiling water, while others have been found to germinate even after having been immersed in liquid Helium (–269° C.) for several hours.

These properties make it very difficult to kill them, and it is indeed fortunate for us that very few disease-producing Bacteria form spores. The most important exception is *Bacillus tetani*, the cause of lock-jaw, which, however, does not enter the blood but remains at the site of the wound which gave it entrance to the body.

BACTERIA AND DISEASE

The first bacterium identified as the cause of a disease was the anthrax bacillus, first observed by Rayer in 1850 and recognized as a micro-organism by Devaine in 1863. These observations were taken up and extended by the great work of Pasteur (Fig. 340), in whose hands the "germ theory" of disease developed into an accepted part of medical science. The number of organisms reputed to cause diseases, of the most varied kinds, extended rapidly, and the multiplication of doubtful claims led Robert Koch, the discoverer of the bacillus of tuberculosis, to formulate four "postulates" or conditions which must be fulfilled before such a claim could be accepted.

FIG. 340.—Portrait of Louis Pasteur.

These postulates are recognized to be the foundation stones of clinical Bacteriology. They are :—

1. The organism must always be associated with the disease.
2. It must be isolated in pure culture.
3. A pure culture inoculated into a healthy and susceptible animal must reproduce the disease.
4. It must be re-isolated in pure culture from the inoculated animal.

At the present time a very large number of diseases, especially fevers, are proved to be of bacterial origin, and the ancient mystery of infection is known to depend on the transference of living Bacteria from man to man, either directly or indirectly. To enter further into the ramifications of medical Bacteriology would, however, be impossible in a textbook of Botany.

Pasteur's interest in Bacteria sprang from his long controversy on the subject of **spontaneous generation.** It was for long supposed that putrefaction was a spontaneous phenomenon, and when it became known that decomposing matter swarmed with microscopic organisms they were believed to have been generated *de novo* in the putrefying substance itself. Despite a number of experiments in the eighteenth and nineteenth centuries which showed that if organic matter were first heated and then protected from the air no decomposition and no generation of organisms resulted, the belief in spontaneous generation persisted almost to our own time. Pasteur, however, gave the idea its death-blow by his clear demonstration that decomposition depended invariably on the presence of material particles (his " germs ") which came from the air. When the air was filtered it lost its power of starting decomposition, while among the particles filtered from the air were many microscopic organisms of the same kinds as those which appeared in the decaying substances.

Pasteur's views and experiments struck the imagination of the great English surgeon Lister, and his application of these resulted in the development of **antiseptic surgery.** He showed that the inflammation or sepsis of wounds was due to Bacteria which gained entrance either from the air or from contamination by dirt, or even from the surgeon's instruments or his skin. He therefore introduced the practice of washing all his instruments in carbolic acid (phenol) and dressing the wound with material soaked in the same substance, thus killing the Bacteria. The air of the operating theatre was likewise disinfected by keeping up a continuous spray of carbolic acid during an operation.

The introduction of these practices saved innumerable lives and removed for ever the fear of surgical gangrene, which had formerly meant a deadly risk in even the simplest operation. The use of chemical antiseptics had serious drawbacks, not only from the point of view of the surgeon, but also in the retardation of healing in the patient. Nowadays the **aseptic method** is used instead. Everything in the operating theatre which will be in contact with the patient is sterilized beforehand by heat and the air is filtered. The only antiseptic used is for cleaning the patient's skin at the site of the incision. Even the surgeon himself is entirely wrapped in sterilized coverings and he wears a sterilized mask and rubber gloves.

Cultivation of Bacteria

The possibility of a science of Bacteriology rests on the power of isolating the different species and examining their properties separately. All the early work was done by cultivation in liquid media, which made isolation well-nigh impossible. The first pure culture, that of a milk organism, was achieved by Lister in 1878, but it was Robert Koch who, in 1881, introduced the technique of culture on a solid substratum, which made isolation simple. He used beef extract containing gelatine, which was poured out on to glass plates and allowed to solidify under a cover. When a liquid containing Bacteria was thinly distributed over a gelatine plate, each individual cell settled on the solid surface and remained stationary, multiplying until a visible mass, or **colony,** was formed (Fig. 341), consisting of a pure strain, all the offspring of one individual. If part of a colony was then transferred to a fresh plate it would increase into a pure culture of that strain. A mixed growth of Bacteria could thus be separated into its constituent species.

Gelatine has the disadvantage that it is liquefied by many species, and it was soon replaced by a carbohydrate, **agar,** obtained from seaweed, which is not easily liquefied and can be combined with any necessary nutrients, generally beef extract and peptone. Both gelatine and liquid media are, however, retained for some special purposes. A second great step forward was the introduction of a form of flat glass basin with a loose lid, called a **Petri dish,** after its inventor, which is used instead of the inconvenient glass plates. The melted agar is poured into the dish while hot and allowed to set, protected from contamination by the lid.

Fig. 341.—A mixed culture of bacteria growing on agar in a Petri dish showing colonies of varying forms.

Bacterial Species

Much controversy has centred around the question of what constitutes a species among Bacteria. The use of chemical criteria as a means of distinguishing them is different from anything accepted in other groups, and it is complicated by the tendency of Bacteria to vary considerably in their chemical activity, not only between different strains but even in one and the same culture at different times.

Many Bacteria when kept in artificial cultures gradually lose some of the chemical powers which they possessed when first isolated, and in addition they may vary morphologically, the type of the colony changing from smooth to rough, or irregular. These changes can often be reversed by appropriate treatment, and are supposed by some to be evidence of a complex and lengthy life-cycle, but they obviously create uncertainties in identification. The great majority of the supposed species described more than thirty years ago are so uncertain as to be valueless, and at the present day it is recognized that only prolonged and detailed study of a particular organism, including a knowledge of its powers of variation, can enable us to say with certainty whether it is a distinct species or not.

The older idea that Bacteria were so variable that the discrimination of species was impossible cannot now be upheld. Most of the important disease-producing organisms are so fully known that their specific character can be accepted with reasonable certainty. Variation is nevertheless a factor of great importance. Some organisms like the nitrogen-fixing bacterium *Azotobacter* and the root-nodule bacillus *Rhizobium* show a definite cycle of changes in the course of their natural lives, so that a knowledge of the full life history is essential to understand them. Many other Bacteria may be in a like case, but all too little is known on the subject.

BACTERIA IN RELATION TO HIGHER PLANTS *

Although we generally associate Bacteria with animal and human diseases, a great many plants are also attacked by them, and many important plant diseases are produced in this way. Bacterial infection most generally takes place through wounds in the host plant. For example, the Olive tubercle caused by *Pseudomonas savastanoi* is frequently found to have been started by wounds caused by hailstones. Certain Bacteria enter the plant through broken roots. In other instances the entrance of the Bacteria is made through natural openings in the tissues, such as the stomata of leaves.

Various agents assist in the transference of disease from one plant to another. Insects, worms and slugs carry Bacteria from diseased to healthy plants, and apart from these the plants themselves may harbour parasites from one year to another in the roots and stems, which re-infect the fresh growth produced in the following spring.

Black Rot of cabbages is transmitted through the seeds, and the so-called " Yellows " disease of Hyacinths is carried in the bulbs. The soil around the plants may be a source of infection, and healthy plants grown in infected soil will in all probability develop disease. Man and animals, especially through the agency of dung heaps, help to spread certain diseases, and birds have been suspected of transmitting some bacterial plant pathogens.

Parasitic Bacteria are frequently followed by saprophytic ones which complete the destruction of the tissues, and the wounds caused by one bacterial disease may enable another and more virulent one to gain admission. In general, Bacteria are unable to enter a plant except through some break in the cell tissue of the host ; they cannot bore their way through a healthy cell wall.

The effect on the host plant varies according to the particular disease.

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* A fuller treatment of bacterial plant pathogens will be found in Volume IV.

Sometimes there is rapid destruction, and an attack seems at least to lessen the growth of the plant. For example, it has been found that tomato plants attacked by *Bacterium solanacearum* only grow to half the size of healthy ones. In other instances the effect of bacterial attack may be to stimulate the growth of certain parts of the plant, whereby abnormal structures are host produced. The Witches' Brooms produced on Pines are now generally attributed to bacterial attack. In other cases the effect of the Bacteria is to produce swelling or **hypertrophy** of the affected parts. One of the most important examples of this is the Crown-gall, caused by *Bacterium* (*Pseudomonas*) *tumefaciens*, which develops on the stems of Apple trees and other plants, where large swellings may be formed, causing great damage (Fig. 342).

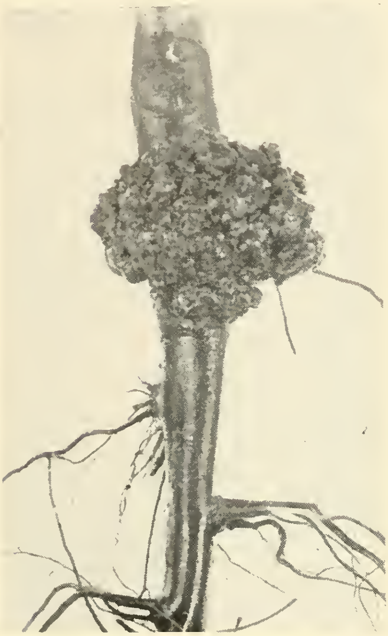

FIG. 342.—Crown-gall on Apple.

Apart from diseases such as we have mentioned, in which serious damage is caused to the host plant, there are others which only produce spots on the foliage and do comparatively little harm.

Certain Bacteria live customarily in plant tissue without causing any apparent damage, in fact, both the bacterium and the host plant appear to derive certain advantages from the union. We speak of a condition in which two individuals of different groups live together to their mutual advantage as **symbiosis,** and we shall consider later other examples of such an arrangement. The root-nodule Bacteria, which we shall discuss shortly (p. 359), can be considered as an example of symbiosis, but we may mention here the case of *Ardisia crenata*. It is a greenhouse plant, grown for its ornamental red berries and thick evergreen foliage. Here the bacterial infection is local and internal. The Bacteria occur most abundantly at the edges of the leaves, where they fill pockets or cavities (Fig. 343). They multiply enough to make the leaf tissues swell and turn yellowish round the cavities, but the tissue is not killed and the leaves do not fall.

Bacteria also occur in other parts of the *Ardisia* plant, particularly in the seeds, and it is by this means that the Bacteria enter fresh plants. If seeds are heated to 60° C. they can be freed from Bacteria and sterile plants raised. These are always crippled and stunted, so that we may conclude that the presence of the Bacteria has become essential to the health of the higher plant. A similar condition is found in certain tropical Rubiaceae belonging to the genera *Psychotria* and *Pavetta*, in which Nitrogen fixation by the Bacteria has been proved (Fig. 344).

Bacterial Antagonism

It has long been known that certain Bacteria and Fungi in cultivation antagonized the growth of others, but the subject assumed practical importance in 1929 with the observations of Fleming on the suppression of *Staphylococcus* by a mould, *Penicillium notatum*. The successful application of this discovery to the treatment of some types of bacterial infection aroused widespread interest in the subject and led to the discovery of many other **antibiotic substances** produced by other moulds and Bacteria. Many of these are too toxic to human subjects to be of medical value, but a few, such as Streptomycin, from *Actinomyces griseus*, a soil organism, promise to rank in value along with Penicillin.

Fig. 343.—*Ardisia crenata*. Leaves with bacterial pustules around the margins.

Fig. 344.—*Psychotria hirtella*. Transverse section of leaf through a bacterial nodule showing hypertrophied cells filled with bacteria.

Many of these substances are formed by soil organisms, and it is probable that they play an important part in the bacteriology of the soil. Indeed it is possible that competition between higher plants in nature is not unconnected with the operation of similar excretions.

BACTERIA IN THE SOIL

The soil is the natural home of myriads of Bacteria, and some of the chemical processes which they carry out are responsible for maintaining soil fertility and are therefore of the greatest importance to us.

It was proved by Boussingault in 1858 that plants are unable to absorb Nitrogen directly from the atmosphere, of which it composes about four-fifths, but that it is absorbed in the form of nitrates from the soil. Nitrates, being very soluble, are easily washed out of the soil by rain and so lost, passing eventually into the sea. This means that fresh supplies of nitrates must be continuously produced if the soil is not to become barren.

These nitrates are obtained in two distinct ways. Firstly, by the decomposition of the proteins of dead organisms to yield ammonia. Very many different kinds of saprophytic Bacteria and Fungi take part in this operation. Secondly, by the fixation of Nitrogen from the air, which also produces ammonia. This is the work of two Bacteria, both endowed with this peculiar power. One is a rounded, coccus-like organism called *Azotobacter chroococcum* (Fig. 345), the other is a spore-bearing anaerobe, *Clostridium pastorianum* (Fig. 346), which finds suitable conditions in the soil humus.

The result of both processes is to produce ammonia. The ammonia is oxidized by a third bacterium, *Nitrosomonas europaea*, to nitrite, while this in turn is oxidized to nitrate by *Nitrobacter winogradskyi*. All these processes are exothermic and the organisms live on the energy got from them, as explained below.

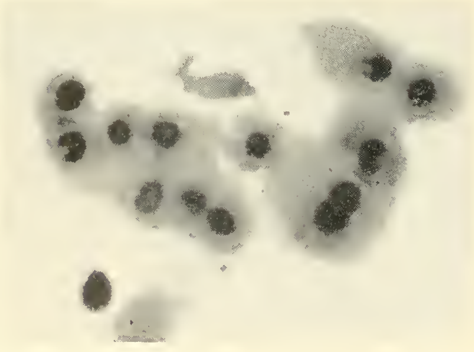

FIG. 345.—*Azotobacter chroococcum.* Cells stained to show the mucilaginous capsule.

There is an opposing process of de-nitrification also at work, however, due to a number of Bacteria which have the power of reducing nitrates, releasing elemental Nitrogen. In healthy soils the process is comparatively slight, but in the sea it operates on a gigantic scale, returning Nitrogen to the atmosphere.

The supply of nitrates thus depends on a chain of bacterial reactions and is subject to complex fluctuations as the result of environmental conditions, especially aeration and acidity. In acid soils, such as peats, it is usually inhibited, while in well-aerated sandy soils it may be twice as active as in close clays.

Boussingault found that plants of the order Leguminosae were apparently exceptions to the general rule, and this is now known to be due to their symbiosis with certain Bacteria, which enter roots from the soil and stimulate the growth of **root nodules** in which the bacteria multiply (Fig. 347). This organism, *Rhizobium*, of which the principal species is *R. leguminosarum* (Fig. 348), has also the power of fixing atmospheric Nitrogen, at least when living in a root, and it appears that the flowering plant benefits by absorption of some of the Nitrogen compounds thus formed. The roots of Leguminosae are consequently particularly rich in Nitrogen, and such crops as Clover, which belongs to this family, have long been known to enrich the ground on which they grow (Fig. 349).

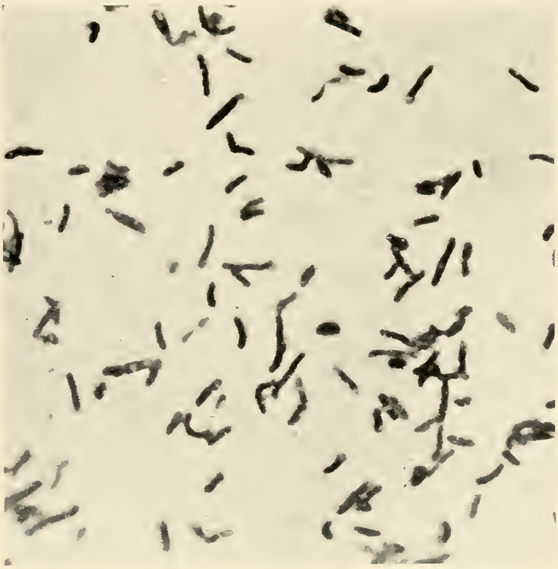

FIG. 346.—*Clostridium pastorianum*. Gram stained.

CHEMOSYNTHETIC BACTERIA

Among the Bacteria there are some which display a very interesting type of metabolism which marks them out as biologically very primitive. This is called **chemosynthesis.** It differs from photosynthesis in that the energy for Carbon assimilation comes not from light but from the oxidation of certain inorganic or simple organic substances. The reactions employed by these Bacteria are all exothermic, that is to say, they yield free energy which is utilized for building up carbohydrates in the cells. These plants are therefore independent both of light and, mostly, of organic matter, so that they would be capable of existence even under the conditions which must

FIG. 347.—Roots of *Trifolium repens* showing nodules produced by *Rhizobium trifolii*.

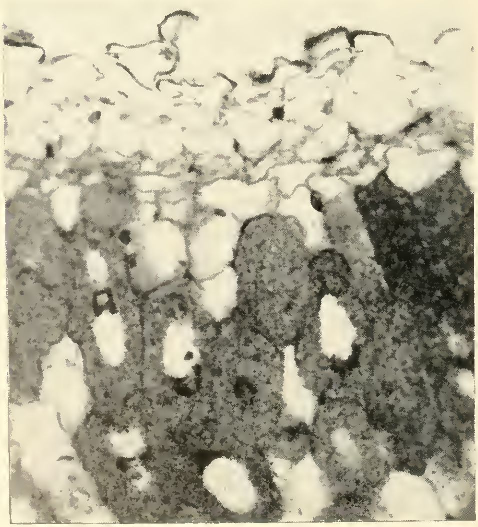

FIG. 348.—Section through part of a bacterial nodule on a root of *Melilotus albus* showing peripheral masses of bacteria in the tissue cells and enlarged cell nuclei.

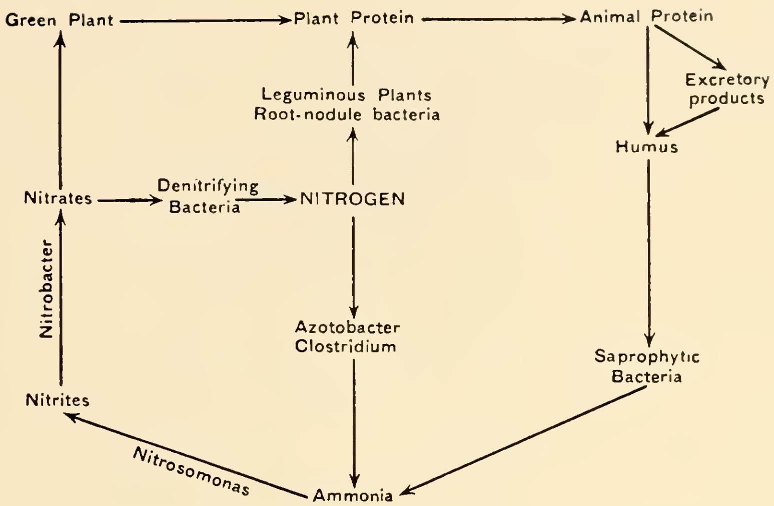

FIG. 349.—Diagram illustrating the circulation of Nitrogen in nature.

have obtained in very early geological ages, when the atmosphere was so densely charged with water vapour as to be opaque, and before other organisms had appeared. The amount of energy obtained in this way does not compare with the amounts available from sunlight, so that photosynthetic organisms have a very great advantage over chemosynthetic ones. Moreover, photosynthesis represents a general gain of energy from outside this planet, while chemosynthesis is a mere exchange of energy between existing terrestrial systems. The soil Bacteria mentioned above form a very important section of this group, though the energy outcome of the reactions involved is not large. The energy release in the oxidation of potassium nitrite to nitrate, for example, is only 22 calories per gram-molecule of nitrite oxidized.

Other reactions which occur are the oxidation of Hydrogen to water, of methane and of Carbon monoxide to Carbon dioxide (especially in bogs) and of Hydrogen sulphide to water.

The latter is characteristic of the colourless Sulphur Bacteria, abundant in natural waters, which play an important part in the purification of sewage. The Sulphur is usually deposited in granules within the cells, but some of it is further oxidized to sulphuric acid. This process is much more energetic than nitrification, the yield being 62 calories per gram-molecule of Hydrogen sulphide and 141 calories per gram-molecule of Sulphur oxidized.

VIRUSES *

It has long been known that some types of " variegation," that is to say, the yellow mottling seen on the leaves of many plants, could be communicated

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* A further treatment of Virus Diseases will be found in Volume IV.

from plant to plant by grafting, and in 1892 it was proved that this was due to a substance which could pass through a fine porcelain filter that held back even the smallest Bacteria. Furthermore an infinitesimal dose of this substance rapidly spread throughout an inoculated plant and apparently increased enormously in amount in doing so. These facts led to the conclusion that the substance in question was a living and growing material, whose particles were too small to be microscopically visible. Thus arose the idea of a " virus " as a type of living organism lying in a region much below the smallest Bacteria. It has since been shown that many of the commonest diseases both of plants and animals are attributable to such filterable viruses, and the subject has advanced to the front rank of importance.

It is a curious fact that we only know of viruses as parasites, that is, we can only recognize their presence by the effects on their hosts. No such thing as a free-living or saprophytic virus is known, and it is difficult to see how they could be discovered if they exist. This argues against the idea, once popular, that viruses are a primitive form of life, lying between the living and the non-living, with particles which are intermediate between large molecules and the smallest visible organisms.

Dilution and filtration experiments with virus-containing juices have proved that there are definite virus particles, which vary between 10 and 200 $m\mu$ in diameter ($m\mu = \frac{1}{1000}\mu$). They vary greatly in their power of resistance. Some are easily killed by drying, heat or poisons. Others will remain active for years in the dry state or survive in absolute alcohol for forty-eight hours. This resistance to agents which normally kill living organisms very rapidly, combined with the fact that some viruses can be apparently precipitated from suspensions and redissolved in water, has suggested doubts whether all viruses are really of the same nature. The belief has been growing that whereas some viruses are possibly ultra-bacteria others are simply toxic substances. The latter view seems to have been definitely proved by the isolation of several viruses in fully crystalline form, and of some others as liquid crystals. Such substances certainly cannot be considered to be living agents. The apparent growth of such viruses in the host plant can only be accounted for by supposing that they catalyze the production of similar molecules in the cells of the host. In this respect their action is analogous to that of the genes in a normal cell.

Among plant diseases caused by viruses are the important group of **mosaics** (Figs. 350 and 351), so called because they cause mottling of the leaf. The contagious variegations first referred to belong to this group. Flowers may also be affected, and the coloured streaking or " blazing " seen on Tulip petals is an example which must be familiar to many. Other viruses cause stunting or malformation of growth, yellowing of leaves, fruit dropping, or crinkling and rolling of leaves (Fig. 352). They are seldom fatal to the host, but they usually cause a marked diminution of vigour which is accompanied by a serious reduction of crop, so that their agricultural effect is immense. They are very seldom transmitted through the seed, but plants like the Potato, which are habitually propagated by vegetative means, carry

FIG. 350.—Mosaic disease on leaf of the cultivated Parsnip.

FIG. 351.—Yellow mosaic on Tobacco caused by the Tobacco mosaic virus.

(*Photographed by Dr K. Smith, F.R.S.*)

the diseases from year to year and become progressively weakened. This is the reason why cultivated strains of Potato have only a limited life and must be replaced at intervals by new seed hybrids which are free from virus. Sometimes a plant may carry a virus without any external symptoms except a general weakening, or it may carry a virus which is only pathogenic for another species. One is led to wonder whether perhaps the mysterious phenomenon of growing old is not due to the continuous effect during life of such mild or hidden viruses in our system.

FIG. 352.—Leaf-roll Virus affecting Potato leaf.

Some viruses can only be transmitted by direct protoplasmic contact, as in grafting and budding, but many are carried by sucking insects, especially aphids, in whose bodies the virus may remain active for many days. The superiority of Scotch Potato seed is due largely to the absence from Scotland of *Myzus persicae*, an aphid which is one of the chief carriers or **vectors** of Potato viruses.

Lastly it may be mentioned that the deliberate infection of certain crop plants by symptomless viruses has been shown to prevent their infection by virulent ones. Whether this is a practical measure or not, it is interesting as the first case of artificial immunization among plants.

Certain peculiar viruses infect even the Bacteria. These viruses, known collectively as **bacteriophages,** enter and destroy the bacterial cells. They are usually specific for particular bacterial species. Resistant individual cells frequently survive attack by the virus and, from these, resistant strains may arise which perpetuate the species.

CHAPTER IX

THE LICHENS

Mention has already been made of the association of Bacteria with parts of flowering plants to their mutual advantage. In the Lichens a similar type of association invariably occurs, only in this instance the association is between an Alga and a Fungus. The Lichens afford the best example of **symbiosis** met with in the plant kingdom. In this symbiosis the Fungus provides the body of the organism, while the Alga, by virtue of the chlorophyll present in its cells, is enabled to manufacture food both for itself and also for the cells of the Fungus body in which it is immersed.

The Lichen thallus, which is essentially fungal in nature, varies considerably in shape, and in some species is highly developed and complex both in form and structure. The reproductive organs too are fungal in character, and by means of them the Lichens can be related to certain well-known fungal families. The algal constituent, on the other hand, is relatively simple. In most it is unicellular, though in a few Lichens it is filamentous.

With very few exceptions the Fungus is a member of the Ascomycetes, and the reproductive bodies are either apothecia or, in certain genera, perithecia. In one or two tropical Lichens the Fungus is a member of the Basidiomycetes. The Alga belongs either to the Chlorophyceae or to the Cyanophyceae, and in the majority of Lichens the algal constituent is a member of either the Chlorococcales or Chaetophorales.

Classification depends chiefly on the form of the fungal element, and the whole group is separated into two main divisions :—

1. **Ascolichenes,** in which the Fungus is an Ascomycete.
    (1) Gymnocarpeae, with apothecia.
    (2) Pyrenocarpeae, with perithecia.

2. **Basidiolichenes** or **Hymenolichenes,** in which the Fungus is a Basidiomycete.

The dual nature of Lichens was not recognized until comparatively recently. As late as 1867 it was thought that they were independent organisms, the Algae being regarded as gonidia or asexual reproductive cells. In that year Schwendener published a paper in which he suggested that the green cells in Lichens might in reality be Algae. He thought that the Fungus acted simply as a parasite and that the Alga was eventually killed by it, though at first it was stimulated to more vigorous growth. This is undoubtedly too simple a view, but the idea of symbiosis was not reached until 1873. Schwendener's "Dual Hypothesis," as it is called, excited great criticism, but in 1871 Rees attempted to put the matter to proof by trying to synthesize a Lichen. For this purpose he took the ascospores of the Lichen *Collema* and sowed them in a pure culture of the Blue-green Alga *Nostoc*. As a result he obtained a Lichen, although he was not able to induce it to fruit. He further observed that the fungal elements died off when no *Nostoc* was forthcoming.

In 1886 Bonnier succeeded in synthesizing various Lichens from the two components and showed that it was possible to obtain fruiting bodies from the association of fungal hyphae and true algal cells taken from the open. Even at the present time it has not been found possible to isolate the Fungus and grow it to maturity in pure culture, except in a single instance in the Basidiolichen *Cora*, where the Fungus, *Thelephora*, is known to occur in nature apart from the Lichen.

The Lichen thallus may be either **homoiomerous** or **heteromerous,** according to whether the algal cells or **gonidia** are scattered uniformly among the fungal elements or whether they are restricted to a single layer. There are three main types of development of the Lichen thalli : **crustaceous,** when they form incrustations on the surface of stones or rocks ; **foliaceous,** when they are flattened and leaf-like ; and **fruticose,** or shrub-like, when they are attached by the base and grow either vertically or pendulous from the point of attachment.

The fungal hyphae are closely woven together into fairly compact " false tissues," and in the best developed species the following strata can be distinguished :—

1. The Upper Cortex of closely compacted hyphae.
2. The Gonidial Layer with algal cells.
3. The Medulla, which is less compact.
4. The Lower Cortex, which is often absent.
5. The Hypothallus, a thin sheet of hyphae which often has a different colour from the rest and persists chiefly at the margins.

One or more of these layers is missing in many species. There is no special surface layer of cells either above or below.

The algal elements are most frequently unicellular Chlorophyceae, which are often difficult to identify. *Chlorella*, which has been proved to be associated with a number of Lichens, is very similar to *Pleurococcus*. It increases within the thallus by means of aplanospores. *Pleurococcus* itself often occurs, and associated genera such as *Cystococcus* and *Palmella* are also found in symbiosis with fungal hyphae forming Lichens. The chief filamentous Alga is *Trentepohlia*, but a curious parasitic filamentous Alga, *Cephaleuros*, is found in the leaf-growing Lichen *Strigula*, which is very common in the tropics. Among the Cyanophyceae are a number of genera which contribute to the formation of Lichens. Mention may be made of *Gleocapsa* among the unicellular types, and of *Nostoc* and *Rivularia* among the filamentous types.

Although the algal constituent is less affected by the symbiosis than the fungal, certain modifications are found ; for example, *Nostoc* sometimes ceases to be filamentous, and *Gleocapsa* loses its blue-green colour. *Trentepohlia* also changes its form in the Lichen thallus but reverts to normal again in free cultivation.

There are certain vegetative structures which are peculiar to the Lichen thallus. The most important are :—

Soredia. They are small rounded bodies that consist of from one to several algal cells closely surrounded by fungal hyphae. When soredia are formed they can usually be recognized as a greyish powder on the upper surface or at the edges of the thallus. They are dispersed by wind and form a method of vegetative propagation, each soredium containing both the Fungus and the Alga together.

Isidia. They are minute stalked outgrowths from the surface of the thallus, which contain both algal and fungal elements. They differ from soredia in being covered with a definite cortex and they are not detachable. They may be photosynthetic in function.

Cephalodia. They are found on the upper surface of some Lichens and develop as abnormal and generally dark-coloured swellings or warts. They are composed of the normal Lichen hyphae but with a different algal constituent. They may be regarded as due to the reaction of the Fungus to another algal partner, and in a few cases a cephalodium may resemble another known Lichen, which presumably has the same fungal constituent.

Cyphellae. They are small roundish cavities scattered over the under surface of certain Lichens. Each has a definite rim and opens into the medulla of the Lichen. Probably their function is to aid aeration, as they occur chiefly in species with both an upper and lower cortex.

REPRODUCTION

With the exception of a few tropical species which belong to the Basidiolichenes, all known Lichens belong to the division Ascolichenes, in which the fungal elements belong to the Ascomycetes, and consequently the reproductive organs are either apothecia or perithecia.

In the simplest or **Lecideine** type the apothecium consists solely of fungal tissue and differs in no striking way from that found in the Ascomycetes, but in the **Lecanorine** type (Fig. 353) the rim of the apothecium has the same structure as the rest of the thallus, including algal cells.

The asci are separated by paraphyses, and the whole of the hymenial surface resembles that found in the Pezizales. Each ascus is of the typical Ascomycete form, and each usually has eight spores which are either simple or septate. Lichen apothecia vary greatly in size and may be anything from 0·25 to 10 mm. or more in diameter. Not infrequently the hymenium is a different colour from the thallus and is sometimes quite brilliantly coloured.

The perithecia also, where they occur, resemble those of the Ascomycetes. A complete hymenial layer may surround the inner surface of the perithecium, or it may develop only around the upper parts. For details of the sexual organs see p. 372.

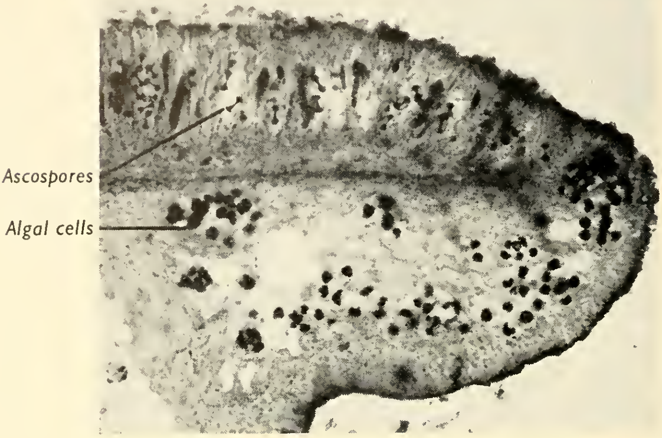

FIG. 353.—*Xanthoria parietina.* Vertical section through part of an apothecium showing thallus tissue below, which forms the margin of the apothecium, and the hymenial layer containing bilocular ascospores.

NUTRITION

In the study of the Lichens special interest is attached to their physiology. In the higher plants food is derived partly from the air in the form of Carbon dioxide and partly from the soil as inorganic compounds. In the Fungi we know that owing to the absence of chlorophyll the organic nutrients cannot be manufactured, and the Fungus becomes either a parasite or a saprophyte in order to overcome this deficiency. The Lichens, owing to symbiosis, are enabled to obtain their food like a flowering plant or, for that matter, like an Alga. In the Lichen thallus the algal cells obtain protection and moisture in the thallus of which they form a part and enjoy conditions under which they can grow rapidly. Probably they assimilate an excess of Carbon dioxide and provide the Fungus with carbohydrates which it uses in its nutrition. The Fungus undoubtedly also consumes the material of dead gonidia and may sometimes invade the living cells.

It is interesting to note that the Lichens are not the only organisms that have evolved this type of symbiosis. There are several cases in the animal kingdom where algal cells are made use of to provide free carbohydrates. In the common *Hydra viridis* we have a simple organism somewhat resembling a minute sea-anemone in which the outer tissues of the body contain algal cells of the genus *Chlorella* (Fig. 354). Another example is found in one of the Nematode worms, *Convoluta roscoffensis.* In this example it has been shown that the worm is unable to live in the absence of its algal symbiote.

In many Lichens there is found to be abundant excretion of Calcium oxalate, which is laid down on the outside of the fungal hyphae. In *Lecanora* *esculenta*, a Lichen living in limestone deserts, it has been shown that these crystals constitute about 60 per cent. of the dry weight of the thallus. Another important group of substances derived from the Lichens are what are termed the **lichen acids.** These substances are sometimes formed in large quantities and are probably directly associated with the peculiar metabolism. One of the most important, chrysophanic acid, gives the bright orange colour to Lichens like *Xanthoria parietina* (Fig. 355), which is so commonly seen on old roofs. Another valuable series of these acids yield the litmus of commerce and the closely similar orchil (orseille). These purple dyes are chiefly extracted from *Roccella tinctoria*, which is common on the rocky coasts of southern Europe (see Volume IV, " Economic Botany ").

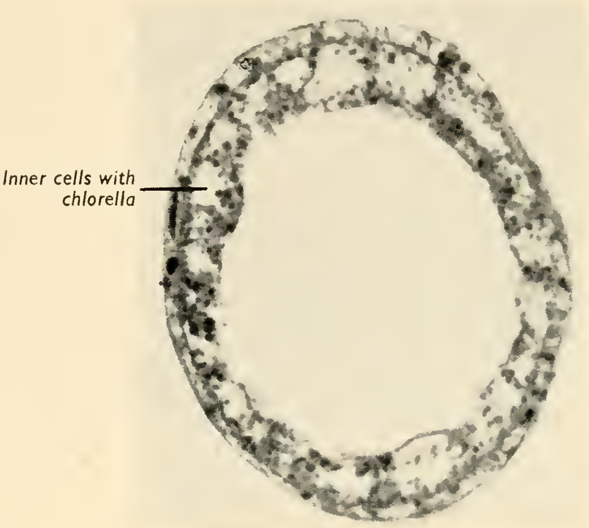

FIG. 354.—*Hydra viridis.* Transverse section coelenteron showing *Chlorella* cells in these tissues.

As an example of a well-developed Lichen we shall consider the common species *Peltigera canina.*

Peltigera canina

This Lichen is found growing in large masses on the surface of mossy banks and rocks (Fig. 356). The thallus is dark olive-green above and almost pure white below. It is dichotomously branched, and down the middle of each branch runs a thickened ridge or vein. The thallus is foliaceous and may be several inches long and about an inch across.

The thallus is made up of a continuous cortex on the upper surface, which in mature parts of the thallus consists of hyphae forming fairly large, broad cells (Fig. 357). These hyphae may be composed of from two to six cells and may continue beyond the surface of the cortex in the form of simple or branched hairs. Apart from these hairs the surface of the thallus is

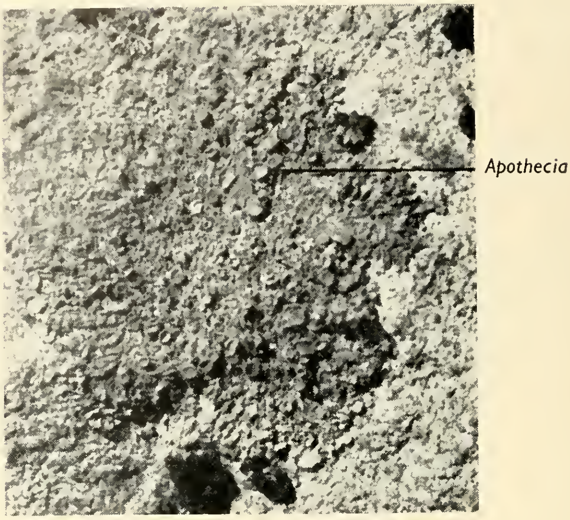

FIG. 355.—*Xanthoria parietina.* Thallus growing on rock showing apothecia. Natural size.

FIG. 356.—*Peltigera canina.* Habit of growth. The upper figure shows the veining on the underside of the thallus. The lower figure shows rolled apothecial lobes protruding from the margins.

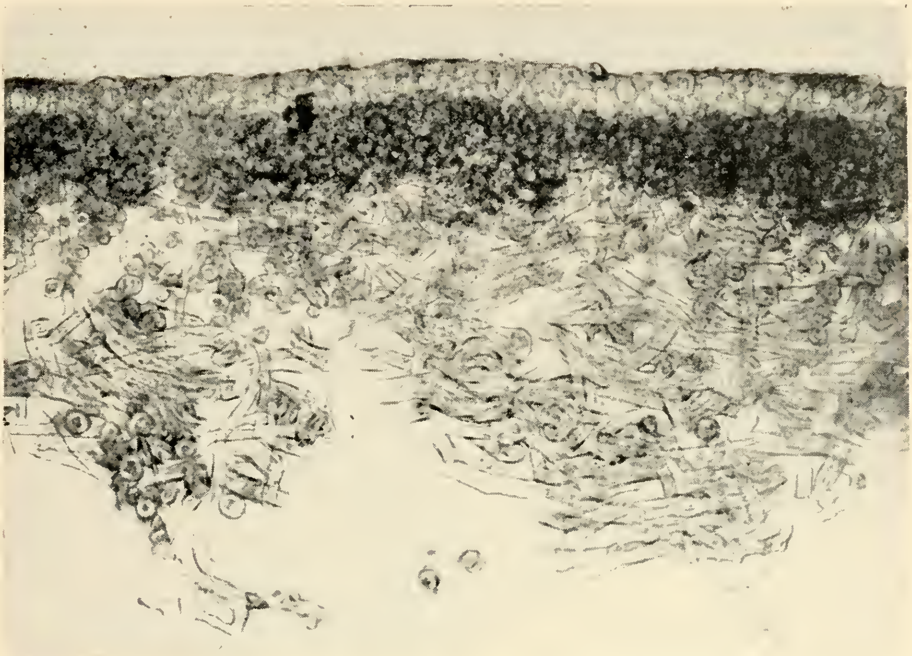

FIG. 357.—*Peltigera canina.* Vertical section of thallus showing colourless cortex at top, below which is the dark gonidial layer and below this the medulla, passing downwards into the loose hypothallus.

somewhat irregular. The cortical tissue is made up of living cells, and though they have lost the power of division they can grow in size and thereby increase the surface of the Lichen as a whole. The cortex is directly continuous with the hyphae of the central tissue, which is called the **medulla,** and with the lower surface, which is termed the **hypothallus.**

The hyphae of the medulla run obliquely in a longitudinal direction, that is, they radiate from the vein towards the margin of the thallus, which they meet at right angles. Between the hyphae of the medulla are large intercellular spaces, whilst the hyphae themselves have thick walls. The medulla becomes very thick in the region of the vein, but may be very thin at the margin.

Between the cortex and the medulla is the **gonidial layer,** which is composed of a mixture of fungal and algal cells, which in this species consist of the Blue-green Alga, *Nostoc punctiforme*, arranged in groups embedded in gelatinous sheaths.

There is no lower cortex ; the hypothallus, which forms the under tissue, consisting of loosely packed cells derived from short and much twisted hyphae. The cortex and the hypothallus are connected together through the medulla by long, straight hyphae, which play an important part in the mechanical support of the thallus and continue throughout its life. Growth takes place at the margin, where cortex, medulla and hypothallus soon become differentiated. Attached to the lower and thicker part of the medulla are small root-like organs termed **rhizinae.** The inner cores of these consist of loosely packed, longitudinal hyphae, which are surrounded by a loose tissue continuous with the hypothallus. These rhizinae are employed partly for attachment, but mainly to absorb water, which they do chiefly by means of the anastomosing hyphae at their apices. Water is passed from them through the veins to the gonidial layer where it is used up during photosynthesis. Our knowledge of the interchange of food between the Alga and the Fungus is still very incomplete.

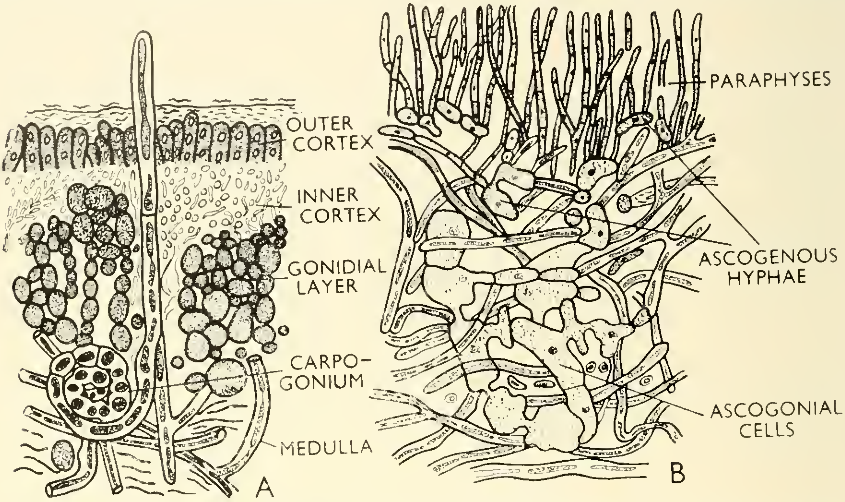

FIG. 358.—A, *Physcia pulverulenta.* Coiled carpogonium and trichogyne before fertilization. B, *Physcia ciliaris.* Ascogonia with developing ascogenous hyphae. (A, *After Darbishire.* B, *After Baur.*)

Peltigera possesses **soredia** and **isidia.** The soredia are small and reproduce the whole Lichen. The isidia develop as outgrowths of the Lichen thallus ; they are developed where conditions are moist and probably have some physiological function. It has been suggested that they assist in increasing Carbon assimilation. One species, *P. aphthosa*, possesses remarkably large, dark-coloured cephalodia, which are scattered over the surface of the thallus.

SEXUAL REPRODUCTION

The apothecia arise from **carpogonia,** which are developed in the medulla of the young lobes of the thallus. Each consists of a coiled multicellular filament of large cells, terminated by a multicellular **trichogyne,** which projects beyond the upper surface of the thallus. The cells of the trichogyne are elongated and have pit connections between them. A number of carpogonia form at each point where an apothecium is developing, though possibly only one becomes fertile. The coiled structure, the absence of auxiliary cells and the multicellular trichogyne are all points which distinguish the Lichen carpogonial system from the somewhat similar structure in the Rhodophyceae (Fig. 358).

Small flask-shaped antheridia, here known as **spermogonia,** are formed on the surface of the thallus, and these produce great numbers of unicellular **spermatia,** that is, non-motile male cells. The spermatia are shed simultaneously in slimy masses. Each spermatium has a cell wall, unlike the corresponding structure in the Rhodophyceae, but they are apparently functional as they are found adhering to the trichogynes, with the terminal cell of which their contents fuse. After fertilization the cells of the trichogyne collapse and **ascogenous hyphae** are produced from the ascogonium, and from them the **asci** develop in a way entirely comparable with that in an Ascomycete, like *Pyronema* (Fig. 359). The details of the nuclear process are not entirely understood. In some Lichens both the trichogyne and the spermatia are absent, and in such cases the ascogonium develops parthenogenetically.

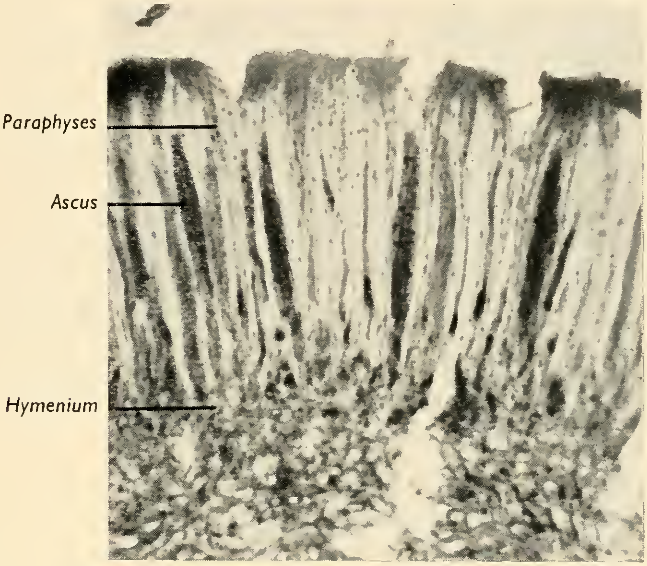

FIG. 359.—*Peltigera canina.* Part of a section through the hymenium of an apothecium showing large asci containing elongated ascospores, and paraphyses which are united above to form a covering layer known as the epithecium.

REPRODUCTION IN THE PYRENOCARPEAE

Verrucaria margacea is an interesting aquatic Lichen growing on stones in running water. The young thallus is pale green, but it becomes dark olive-brown and almost black with age. The algal constituent is a form of *Pleurococcus.* The fungus forms a compact pseudoparenchymatous network, absolutely uniform in structure throughout the thallus. The **perithecia** are immersed in elevations of the thallus and are characterized by a firm black peridium. Paraphyses line the inside of the **ostiole** and the upper portion of the perithecium, and from its base asci containing ascospores are developed in the usual manner. The spores are unicellular at first, but later become septate. They often germinate while still in the perithecium, and the resulting hyphal network is later expelled through the ostiole and floats freely in the water. Such a structure doubtless serves to entrap free-floating cells of *Pleurococcus*, and it may be a specialization to ensure the union of the two constituents.

Distribution

Two factors have to be taken into consideration in relation to Lichen distribution. In the first place there is the peculiar symbiotic life, which we have already referred to, and secondly there is the method of dispersal.

The ascospores are purely fungal structures, so that the possibility of their producing a new Lichen of the same species depends on their encountering the requisite Alga. Lichens, however, also spread by means of small portions of the thallus, which we have described as soredia, while in some Lichens small nodular excrescences become detached and blown about by the wind, as, for example, in *Lecanora esculenta*, the so-called Manna Lichen (Fig. 360). In these ways both constituents are dispersed together, and there is no doubt that in many species these are the most efficient means of dispersal.

Geographically Lichens are one of the most widely distributed groups of plants, many genera and some species having an almost world-wide range. In cold climates they are predominantly, though by no means exclusively, **saxicoles,** that is, rock or stone-livers, while in the tropics, on the other hand, **corticoles,** or bark-livers, predominate and may seriously encumber the trunks and branches of trees. Individuals may be more luxuriant in warm climates, but the number of species is much greater in cold regions, and indeed Lichen growth becomes more and more prominent in the vegetation as one travels away from the tropics. In the far north, beyond the geographical limit of forests, lies the tundra, an immense stretch of heath-like country where, in many places, Mosses and Lichens form the only covering. Here the Reindeer Moss (*Cladonia rangiferina*) is one of the chief Lichens (Fig. 361). It is a fruticose Lichen which is eaten as herbage by the reindeer herds, and it is collected into barns by the Lapps for winter forage.

Lichens may claim to be found farther north and farther south and at higher altitudes on the earth's surface than any other plants. They are essentially pioneers. On fresh rock surfaces Lichens are the first plants to appear. The humus which they accumulate becomes a breeding ground for the spores of Mosses, and this leads on eventually to colonization by flowering plants. The crustaceous forms are usually the earliest to appear and they are followed by foliaceous types. The fruticose forms are usually the culminating development. At each stage certain species are commonly found together, so that Lichen " associations " may be recognized, like those which are formed among higher plants. The character of these associations is largely determined by the nature of the substratum. Thus limestone rocks produce a different set of species from igneous rocks, and the manuring of certain rocks by birds stimulates the appearance of yet another association of nitrophilous species.

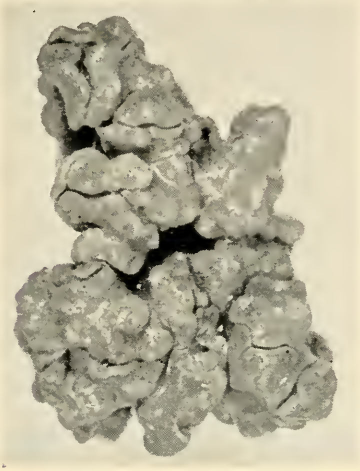

Fig. 360.—*Lecanora esculenta.* The Manna Lichen.
(*From a specimen lent by the British Museum.*)

Fig. 361.—*Cladonia rangiferina* var. *alpestris* showing the fruticose thallus.

On limestones some species may burrow into the substratum of the rock by means of excreted carbonic acid, in such a fashion that the vegetative parts are invisible and only the apothecia, sunk in tiny craters, appear at the surface.

Cliffs facing the sea usually show a marked zonation of Lichens parallel to high-water mark (Fig. 362). At the base of the cliff, where frequently submerged, the rocks are dappled with dark, crustaceous species of *Verrucaria*, especially *V. maura.* Above this there may be a zone of the black fruticose, *Lichina vulgaris.* Higher still, in the zone only reached by occasional spray, is the brilliant orange belt of *Xanthoria parietina*, and finally, on the western coasts of Britain, comes a broad stretch of the grey fruticose *Ramalina scopulorum.*

Lichens are able to withstand great desiccation without injury. For example, *Peltigera* in dry weather may lose all but 5 per cent. of the water which it holds when saturated. Most Lichens can absorb water directly from damp air, but they do not attain in this manner more than 70 per cent. of their saturation content.

When one compares the biological characteristics of Lichens and of the Fungi, it is surprising how opposite they are, considering that the fungal

FIG. 362.—Lichen zonation on a foreshore. Dark-coloured *Verrucaria* below and light-coloured *Xanthoria* above. Aberthaw, Glam.

partner in the Lichen is dominant. We may express the opposition in parallel columns :—

Fungi	*Lichens*
Best developed in warm countries.	Best developed in cold climates.
Mostly of delicate texture.	Generally of very tough texture.
Prefer shade.	Prefer sun.
Demand much moisture.	Can withstand great drought.
Thrive in vitiated air.	Demand pure air.
Grow rapidly.	Grow very slowly.
Predominantly uncoloured.	Highly pigmented.
Develop secondarily.	Usually pioneers.

Lastly we may mention that Lichens have sometimes been used as food. The Iceland Moss, *Cetraria islandica*, is the best-known case. Boiled with twenty times its bulk of water it yields a stiff jelly which is about 37 per cent. digestible. Du Chaillu records that in the famine of 1867 this became one of the staple foods of the Scandinavian peasants. A leathery *Umbilicaria*, known as " Rock Tripe," has also sometimes been resorted to by explorers in an extremity, but it is very indigestible and has little to recommend it.

CHAPTER X

THE CHAROPHYTA

The Charophyta are a small but important group of plants which show marked differences from both the Thallophyta and the Bryophyta.

They are all specialized water plants with a highly peculiar structure and complex reproductive organs. Chlorophyll is the only pigment they possess, and they may be related to the Chlorophyceae ; in fact some authorities have relegated them to that group as a separate order. The older view, and one which still has much to recommend it, was to regard them as a separate phylum, of equal rank with the Thallophyta, whose relationship to other phyla was unknown.

The species are distributed throughout the world, but are most common in the warm and cool temperate zones. It may be mentioned that plants with a wide geographical distribution are often known to be of greater antiquity than those of restricted distribution, and the Charophyta are no exception to this rule, for remains of them are found as far back as the Devonian and Carboniferous rocks. Such forms differ little from the present-day types and throw no light on the ancestry of the group.

Because of the fact that they are common and widely distributed they have been known from early times and were used by many early botanists as material for study and demonstration. For example, the cyclosis of cytoplasm was first demonstrated in the cells of *Chara* by Amici in 1818.

The Charophyta are plants whose stems are either green or grey; the latter occurs in many species, resulting from the masking of the green colour by incrustations of lime on the walls. The main stems are slender and slightly branched. Lateral branchlets occur in whorls at regular intervals up the stem. The reproductive organs consist of antheridia and oogonia, though the structure of these organs differs considerably from the corresponding organs in the Algae. As a result of fertilization a protonema is formed from which the sexual plant is developed.

The plants are submerged, and occur widely in fresh water or water containing less than 1 per cent. of salt. Thus they are found in the Baltic Sea, but not in other more saline waters. The water must be still, or only slow-flowing. There must be no pollution due to sewage, and the plants must be exposed to bright light. They are frequently found in water charged with calcareous material.

The phylum contains only one family, Characeae, with six genera and about two hundred species. We shall consider only one example, *Chara fragilis* ; since the differences between the genera are small this species may be considered typical of the whole group.

Chara fragilis (The Stonewort)

The plant grows to a height of about a foot, though some other species are considerably smaller (Fig. 363). It consists of an erect, somewhat sparsely branched stem, which bears whorls of short lateral branches produced at nodes, which consist of a transverse layer of small cells. The internodes between them are either made up of a single giant cell, or composed of a single central cell surrounded by a number of peripheral cells, which grow over it and are derived from the nodes above and below. The laterals themselves are of limited growth and often produce shorter secondary laterals, so that the whole structure comes to resemble an *Equisetum* ; which accounts for the fact that as early as 1660 John Ray regarded the group as aquatic Horsetails.

Fig. 363.—*Chara fragilis.* Vegetative shoots with branches. Natural size.

Growth is brought about by means of a dome-shaped **apical cell,** which cuts off a series of segments parallel to its flat base (Fig. 364). Each segment divides horizontally into two cells, of which the upper gives rise to a **node** and the lower to an **internode.** The nodal cell divides into a series of cells, consisting of a definite number of peripheral ones and a small number, generally two, central ones. These peripheral cells then function as apical cells and form the **lateral branches of limited growth**. The number of these laterals is therefore determined by the number of peripheral segments, and is a constant for each species. Each lateral now develops by the division of its apical cell in a way identical to that of the main stem, but the internodes remain relatively short, and the whole branch is of strictly limited growth. The secondary laterals which it produces are shorter still, and in both cases the apical cells soon cease to divide and then elongate, forming pointed terminal cells. In successive whorls the individual laterals alternate.

Branches of unlimited growth arise from the lowest or **basal cells** of the first node formed on the laterals of limited growth, and it is also from these cells that the cortications arise which cover the internodal cell of the main stem (Fig. 364). Such **cortications** are characteristic of all species of *Chara.* The cortications arise from cells of the basal branch-node, which divide to give a series of small cells, some of which grow upwards over the internodal cell of the internode above, while the others grow down over the internodal cell below. As they develop they not only keep pace with the elongation of the internodal cell, but also join up with the series of cortical cells growing from the next node. In this way each internodal cell becomes covered with a layer of cells derived from both the upper and lower nodes. These cortical filaments themselves exhibit apical growth and become differentiated into nodes and internodes. The form of the cortications differs in the various species, and is much more elaborate in some than in others. The laterals of limited growth may become corticated as well as the main stem.

The peripheral cells of the lower nodes also give rise to **rhizoids** with apical growth. These rhizoids possess oblique septa, but are not differentiated into nodes and internodes. They branch by a complex process involving the formation of a group of four lateral cells, from the lower pair of which secondary rhizoids may be given off. This process may be repeated.

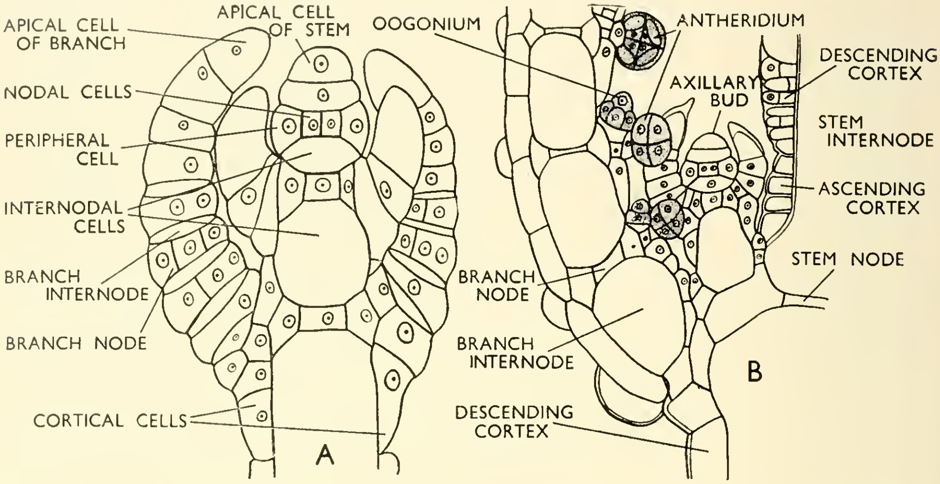

FIG. 364.—*Chara fragilis.* A, Apex of axis, showing apical cell and differentiation of branches. B, Branch axil on an older stem showing axillary bud and young reproductive organs. (*After Sachs.*)

Finally, also from the basal node of the laterals, there may arise **stipuloids,** which are unicellular outgrowths. Either a single row or a double row may be formed. The cells are oval or pointed in shape, and the lower row is directed downwards, while if a second row is present its cells will be directed upwards over the lateral branches. The shape of the stipuloids is a specific character.

CELL STRUCTURE

The cells of the nodes are relatively small, with dense, granular protoplasm and a single nucleus. There are numerous small discoid chloroplasts, which are disposed around the periphery of the cells. No pyrenoids are present. The large internodal cells are sometimes multinucleate, and their nuclei often possess large nucleoli and scanty chromatin. In these cells the cytoplasm forms only a peripheral layer with a large central vacuole. The cell walls are composed of cellulose, though there may be also a superficial layer of a more gelatinous material of unknown composition.

The storage material is starch, except in the oospore, where oil also occurs. This starch also accumulates in special storage structures, termed **bulbils,** which consist of rounded cells of varying size which are developed in clusters on the lower stem and root nodes. They are mainly developed when plants are growing in fine slimy mud.

Sexual Reproduction

In their reproductive organs the Characeae show a high degree of specialization, and the structure of these bodies is unlike anything in other phyla of the Plant Kingdom. The female organ is a large oval structure with an envelope of spirally arranged, bright green filaments of cells. It is termed an **oogonium.** The male organ is also large, bright yellow or red in colour, spherical in shape, and is usually termed an **antheridium,** though some workers regard it as a multiple structure rather than a single organ.

The sex organs are developed in pairs from the adaxial nodal cell at the upper nodes of the primary lateral branches, the oogonium being formed above the antheridium. They are sufficiently large to be easily seen with the naked eye, especially the bright orange or red antheridium. Many species are dioecious. In others the monoecious condition is complicated by the development of the antheridium before the formation of the oogonium, thus preventing fertilization by antherozoids of the same plant. In this case the two types of sex organs usually arise from different points on the lateral branches.

The Antheridium

The antheridium usually takes the place of the oldest secondary branch at a node on a primary lateral, thus occupying an adaxial position on the primary lateral. The peripheral nodal cell which is about to form an antheridium cuts off one or two discoid cells at its base and becomes spherical (Fig. 365). The apical cell then becomes divided into eight cells grouped in an octant. Each of these cells divides into a row of three radially superimposed cells, of which only the innermost cell undergoes any further division. The eight external cells enlarge and are transformed into large curved plates, termed **shields,** thus forming the wall of the antheridium surrounding an internal cavity. They have curved surfaces and their adjacent walls become folded, so that the joints appear as a series of sutures fitting into one another, and give the appearance in longitudinal section of being multicellular. As these shield cells increase in size they become filled with red or yellow pigment, and thus give the characteristic colour to the antheridium. The antheridium is supported on the basal cells, the uppermost of which may elongate and push into the cavity of the antheridium.

Meanwhile the middle cell of each primary segment of the octant elongates, thus carrying the inner cell towards the centre of the antheridial

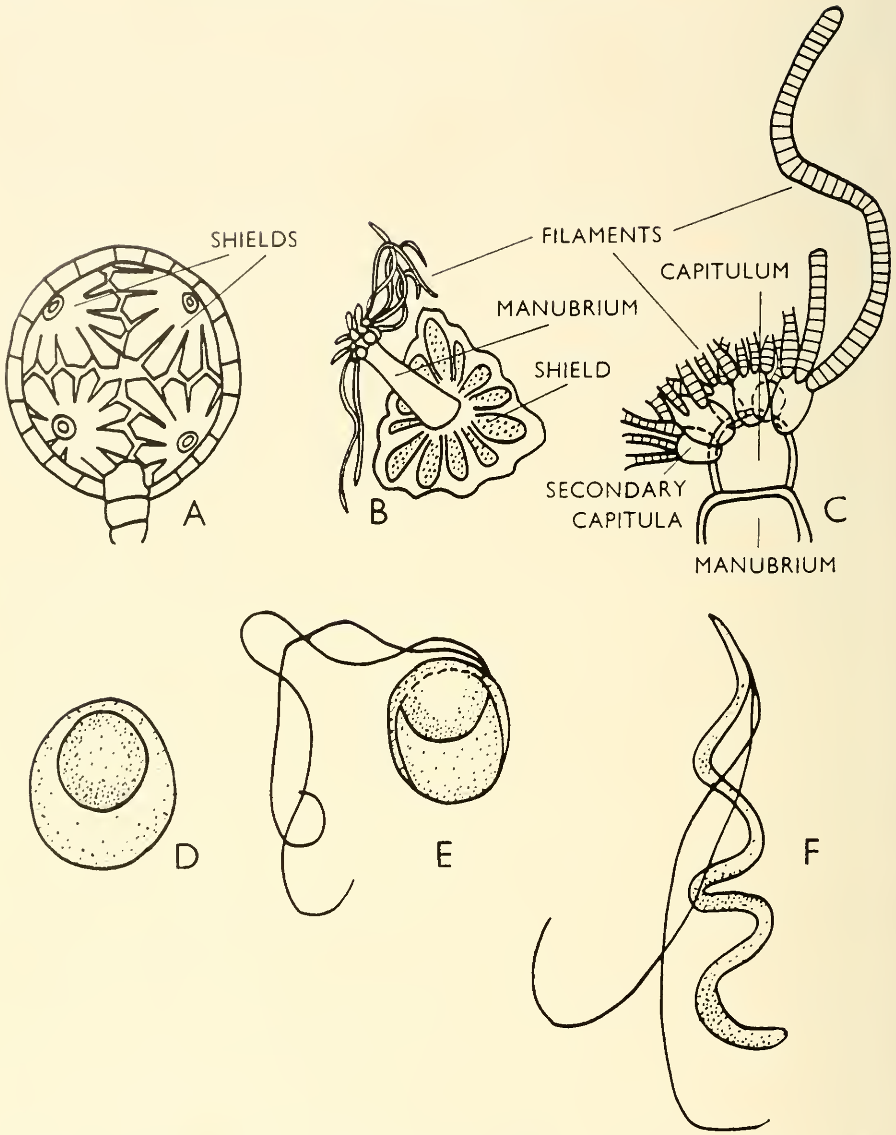

Fig. 365.—Structure of the antheridium. *Chara hispida.* A, Mature antheridium. *Chara tomentosa.* B, Shield with manubrium and filaments attached. C, Head of manubrium showing capitulum and sporogenous filaments. (*After Prosper*). *Chara sp.* D to F, Development of the antherozoid from a cell of a spermatogenous filament. (*After Guignard.*) (*From Grove and Bullock Webster.*)

cavity. The result is the formation of a rod-shaped cell, termed the **manubrium.** One end is attached to the centre of the shield, while at the other is the innermost cell of the series, which now divides and forms the **capitulum** (Fig. 366).

Each capitulum now buds off a group of about four to six cells, which are termed the **secondary capitula.** Each secondary capitulum cuts off

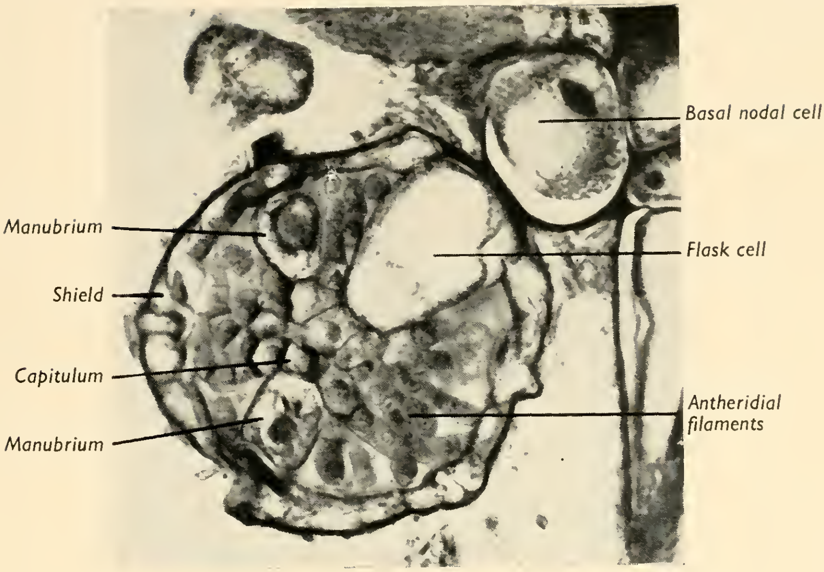

FIG. 366.—*Chara fragilis*. Section of a developing antheridium showing early stages of the spermatogenous filaments. The flask cell is the uppermost basal cell.

two or four **terminal cells.** From these terminal cells, as a result of repeated division, two or four long filaments consisting of from 100 to 200 tiny cells are produced. These are termed the **spermatogenous filaments** ; each cell of the filament functions as an **antherozoid mother cell,** and from it a single **antherozoid** is liberated (Fig. 367). The antherozoid is a small spiral, rod-shaped structure with a single pair of flagella attached near the apical end. The antherozoids are liberated by the falling apart of the shields which form the antheridial wall, and the subsequent gelatinization of the walls of the mother cells.

The enormous production of antherozoids will be realised if we consider that there are eight manubria in each antheridium, and that each manubrium produces six capitula, which give rise to either two or four filaments of spermatogenous cells. Taking the highest number in each case this means the liberation of nearly 40,000 antherozoids from a single antheridium.

It has been suggested, as has already been mentioned, that the antheridium may really be a compound structure and that each cell of the primary octant represents a secondary lateral branch of an antheridial axis, which divides into three cells, the shield, manubrium and capitulum. Of these cells the manubrium represents an internodal cell and elongates, as do such internodal cells, while the capitulum corresponds to the basal node of the secondary lateral and bears spermatogenous filaments, just as basal nodes in the vegetative parts bear cortical filaments. Thus, by this interpretation, the cells of the spermatogenous filaments may be regarded as single-celled antheridia comparable to those in many Algae.

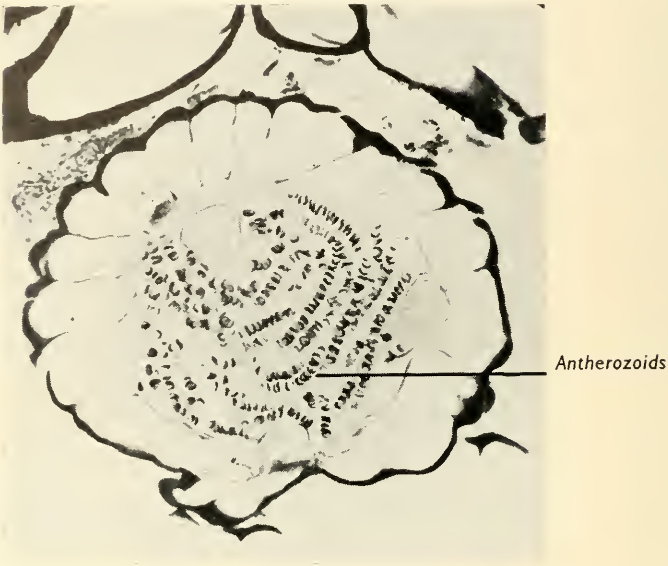

FIG. 367.—*Chara fragilis.* Section of a mature antheridium, showing antherozoids coiled in the cells of the spermatogenous filaments.

THE OOGONIUM

In many species the same basal cell of the node which gave rise to the antheridium may also give rise to the oogonium. This cell divides into two, the lower being the **nodal cell** and the upper the **oosphere** (Fig. 368). From the periphery of the nodal cell five segments are cut off, forming a group of cells which grow outwards and upwards till they envelop the oosphere. The oosphere elongates and becomes oval in shape, while these **enveloping cells** keep pace with its growth. Meanwhile these cells each divide into two by cutting off at the top a cell, which together form a tier of five cells, termed the **coronula.**

At the same time the oosphere has cut off below a basal cell, which is termed the **turning cell.** With the aid of this turning cell the oosphere rotates so that the enveloping cells, which are adherent to it at the top, are spirally twisted, always in a clockwise direction (Fig. 369). The enveloping cells thus serve as a protective tissue around the oosphere, though it is difficult to see the purpose of the spiral twisting unless it be to tighten their contact with the cell inside and with each other. Gelatinous material appears at the top of the oogonium, between the cells of the coronula and the oosphere, and it may be that the twisting movement assists in its extrusion.

Shortly before fertilization the inner walls of the enveloping cells become dilated and push the cells of the coronula apart, thus leaving a narrow neck down which the antherozoids find their way. The wall of the oosphere becomes gelatinous, and the nucleus of the antherozoid, after entry, fuses

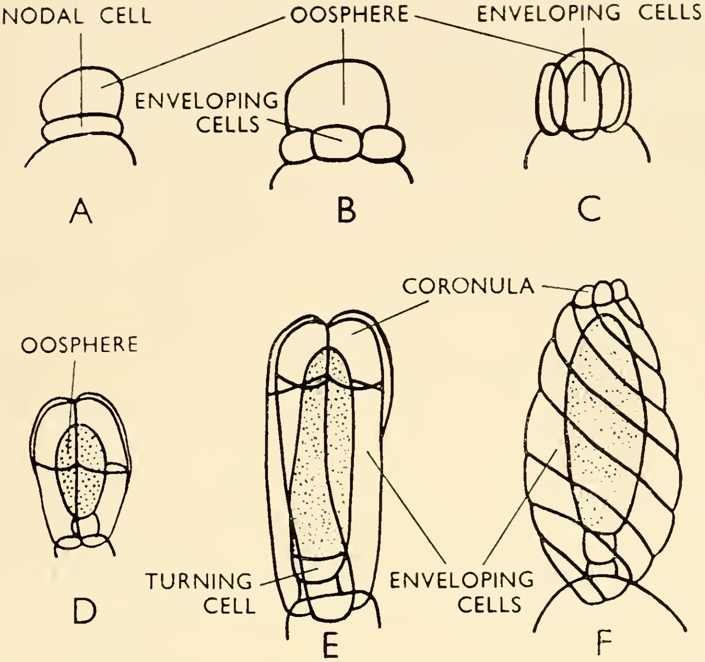

FIG. 368.—*Chara vulgaris.* Development of the oogonium. A, Formation of oosphere. B and C, Origin of the enveloping cells. D, Septation of enveloping cells to form coronula. E, Twisting of enveloping cells. F, Mature oogonium. (*After de Bary and Migula.*)

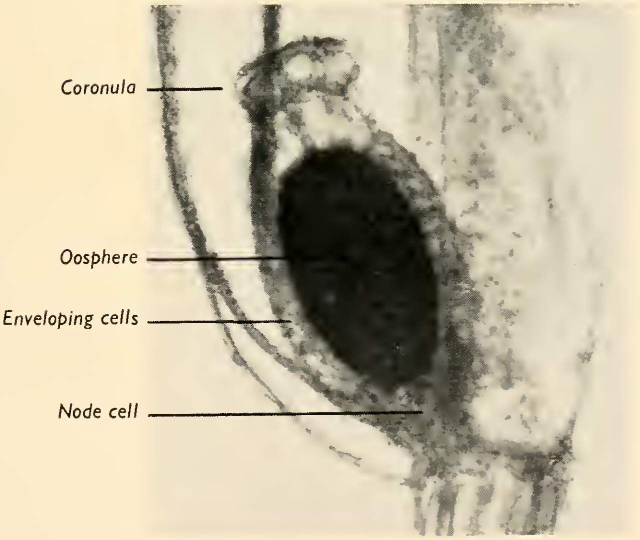

FIG. 369.—*Chara fragilis.* Mature oogonium containing an oosphere.

with the nucleus of the oosphere. In one species parthenogenesis occurs in nature, while it has been artificially induced in others.

After fertilization the zygote nucleus passes to the apex of the oosphere, which secretes a cellulose wall and becomes an **oospore** with a yellow or brownish coloration. It is still enclosed in the enveloping cells which now contribute to the wall of the oospore. Their inner walls become suberized, while the outer walls form the sculpturing on the surface of the oospore. Lime is also deposited, so that the mature oospore is a very resistant structure. At this stage the oospore is shed, and contains both starch and oil as food reserves.

Development of the Protonema

The reserve of food material in the oospore recedes to its basal end, while the nucleus passes to the apical end and divides by two successive divisions, which are thought to be reductional, to give four nuclei. A septum now appears and cuts off one of these nuclei in an apical cell, while the other three disintegrate. The enveloping wall bursts into five or six segments to expose this upper cell, which then divides longitudinally into two cells, which elongate and grow in opposite directions to form the primary **rhizoid** and **protonema** respectively (Fig. 370). This protonema becomes green and undergoes repeated transverse division into a filament of cells. Of these, the lowest undergoes no division and remains colourless. It is regarded as the **basal cell,** but it elongates, thus carrying the remaining cells up with it. Above this are at first three cells, which are the **root-node cell,** the **internodal cell** and the **stem-node cell** respectively.

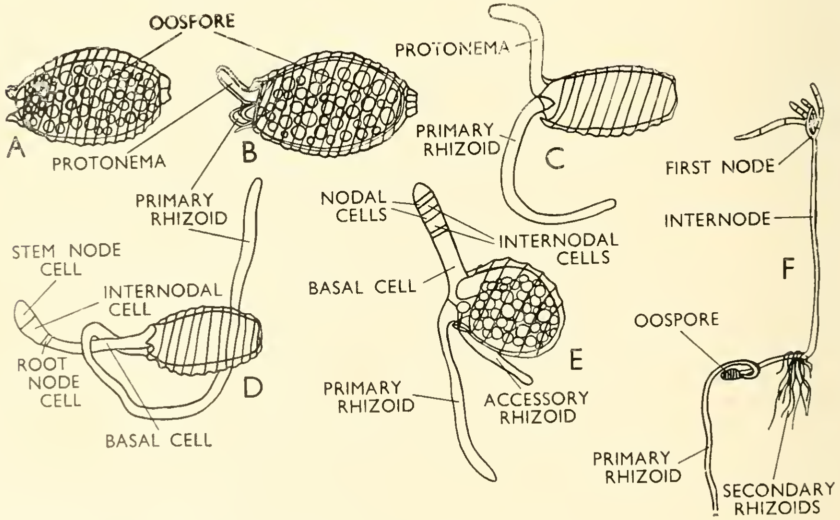

Fig. 370.—*Chara vulgaris.* A and B, Early stages in the germination of the oospore. *Chara canescens.* C and D, Growth of protonema and primary rhizoid and the differentiation of the embryo. *Tolypella glomerata.* E, Septation of embryo and formation of accessory rhizoid. *Chara fragilis.* F, Fully developed embryo. (*From Grove and Bullock Webster.*)

From the root-node cell a number of rhizoids are formed which supplement the primary rhizoid formed by the first division of the germinating oospore. The internodal cell elongates and carries up the stem-node cell, above which the protonema terminates in a short row of cells. The stem-node cuts off in sequence a ring of peripheral cells. From these a whorl of lateral filaments of very limited growth is formed, with the exception of the oldest of the peripheral cells, which cuts off an apical cell, which then divides to form the segments of a new sexual plant. Thus the sexual plant arises as a lateral bud of the protonema in a way not unlike what we have already described in *Batrachospermum*, and resembling the process we shall see later in the Bryophyta, though it must be clearly realised that there is no homology between the structures in the two cases.

VEGETATIVE PROPAGATION

At almost any stage in the life of *Chara* vegetative propagation can occur. Secondary protonemata may develop even more rapidly than primary ones. Fragments of nodes, dormant cells of plants after hibernation or the basal nodes of primary rhizoids may all produce these secondary protonemata, from which fresh sexual plants can arise. It is probably this power of vegetative propagation which explains the fact that species of *Chara* are generally found forming dense mats in the beds of ponds or streams, covering quite large areas.

It will be seen that very little comparison can be made between this and any other group of plants. That the Characeae are highly specialized is obvious, yet it is noteworthy that a fundamentally simple system of cellular nodes and internodes has been modified and adapted to serve very varied purposes in a striking and unique manner.

The life-cycle of *Chara* may be graphically represented by Fig. 371.

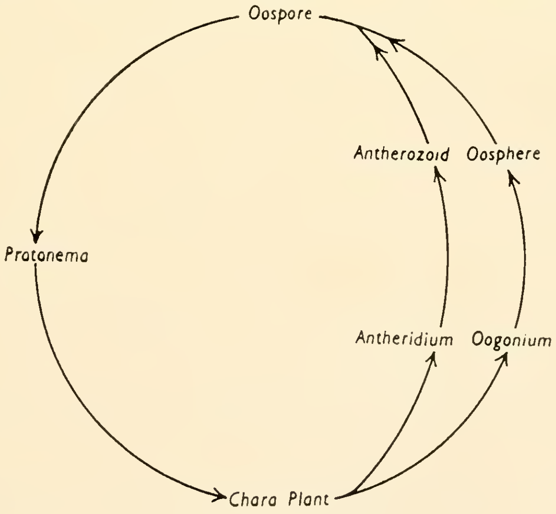

FIG. 371.—Life-cycle of *Chara*.

CHAPTER XI

THE BRYOPHYTA: HEPATICAE, THE LIVERWORTS

WITH the exception of the higher Fungi, which lead a very specialized life, the Thallophyta and Charophyta are essentially aquatic plants. Even in the few instances where a terrestrial habitat has been adopted the reproductive bodies rely upon water for their distribution.

When we turn to consider the Bryophyta we come to a group of plants which are essentially land-inhabiting organisms. Although they still rely to some extent upon water for the movement of their gametes, in their vegetative structure they have adapted themselves to a terrestrial life. They have been likened to the Amphibia of the Animal Kingdom, and this simile is extremely apt in so far as their mode of living is concerned.

If the view is held that plant life originated in the water, the migration from the water to the land must have been a very gradual one. Due possibly to increased competition in the water, plants gradually adapted themselves to colonizing the damp soil at the edge of the water, whence they migrated further and further on to the land, relying on the rain and dew to supply them with the water necessary for life. We can picture this gradual migration, but it must be confessed that we have very little direct evidence for it. One of the largest gaps in the evolutionary sequence of plants is that which separates the Thallophyta from the Bryophyta. Since the transitional types would be necessarily small delicate organisms, it is hardly to be expected that any of their remains would be handed down to us in fossil form. On the other hand, we might have expected to find among the present-day forms some types which could be termed " living fossils," in which the primitive characters of the intermediate or " bridging " species were still retained. This is not the case, and we are left to conjecture what these intermediate types might have looked like.

Turning to the consideration of the Bryophyta as a whole, they may be described as plants in which the body is of fairly simple structure, developing, at least in the simpler members, a flat thallus resembling in vegetative structure that of some of the Thallophyta but showing a marked advance in the method of reproduction. The most important advance has been the retention of the female gamete within a female organ with a cellular wall and neck. This gamete, the **oosphere,** is not set free as in such Algae as *Dictyota* or *Fucus*, but remains enclosed in the female organ, the **archegonium,** and is fertilized by an actively motile **antherozoid.** Moreover, the **embryo** which develops as a result of fertilization is not liberated but remains attached to the parent plant, being nourished by it through an attaching organ or **foot.** This embryo differs from the parent in that it is diploid and that it develops a **theca** or **capsule** containing asexual **spores.** In the production of these spores meiosis occurs and the monoploid condition is re-established. In the Bryophyta this sporophyte never becomes independent, but remains attached to the gametophyte throughout its life, although by producing chloroplasts, as it does in Mosses, it provides to some extent its own food. In general terms, we may say that the gametophyte, which is the principal phase of the Bryophyte plant, produces a sporophyte which lives parasitically upon it. This sporophyte of the Bryophyta is called the **sporogonium** and it produces the capsule in which the spores develop.

The type of alternation of generations found in the Bryophyta, where the two generations are different morphologically, is spoken of as **heterologous,** whereas the type seen in *Dictyota*, where both generations are structurally identical, is called **homologous.**

As we pass from the Bryophyta through the subsequent phyla we shall find a gradual reduction in the importance of the gametophyte and a corresponding increase in the complexity of the sporophyte, until in the Flowering Plants the whole plant is a sporophyte and the gametophyte is reduced to a minute structure enclosed within it.

The Bryophyta comprise the Mosses and the Liverworts and are divided botanically into two classes :—

1. **Hepaticae,** the Liverworts.
2. **Musci,** the Mosses.

HEPATICAE

The Hepaticae are Bryophyta in which the plant is always dorsiventral and is frequently prostrate and thalloid, while the spores are developed in relatively simple **sporogonia** without chlorophyll, except in the Anthocerotales. In the simpler members the thallus is flat, prostrate and dichotomously branched, and secured to the ground by simple processes called **rhizoids.** Some of the more advanced members develop an axis on which leaves are produced. They are included in the order Jungermanniales, as the Foliose Liverworts.

The members of the Hepaticae grow chiefly in damp, shady situations, by the edge of streams, on marshy ground and a few in the water. Very few can withstand serious desiccation and they do not like dry habitats.

The sex organs consist of antheridia and archegonia and may be produced on the same or on different plants. The sporogonium, as we have seen, develops from the archegonium as a result of fertilization and lives for a time as a parasite. In it the spores are developed, from which fresh plants are produced. Some species develop detachable vegetative organs termed **gemmae,** small multicellular bodies which after liberation can develop into fresh plants.

The Liverworts are geologically an ancient group, fossil remains of which are known from as far back as the Coal Measures.

They are divided into four orders of which we shall consider examples from the following three :—

1. **Jungermanniales** (*e.g.*, *Pellia*).
2. **Marchantiales** (*e.g.*, *Marchantia*).
3. **Anthocerotales** (*e.g.*, *Anthoceros*).

Jungermanniales

The Jungermanniales are Hepaticae in which the thallus is never differentiated into distinct layers of tissue, and pores are never present. The rhizoids are of one kind, unicellular, and always smooth-walled. The sex organs are arranged in groups on the thallus or its branches, though in the latter case these branches are not morphologically specialized as in the Marchantiales. The sporogonium is often provided with a long stalk bearing a capsule which dehisces by four valves.

This order is the largest of the Hepaticae and is subdivided into two sub-orders : **Anacrogynae,** mostly thallose, in which the archegonia arise from behind the apical cell, and **Acrogynae,** mostly foliose, in which the archegonia arise from the apical cell itself.

We shall consider one example of the order, *Pellia epiphylla*, which is a member of the Anacrogynae.

Pellia epiphylla

Pellia epiphylla occurs commonly throughout the country by the sides of streams, in damp woods and under hedges. Occasionally it appears on old humus-laden sand dunes. It consists of a flat, lobed thallus which branches repeatedly, so that the lobes often overlap one another (Fig. 372). Moreover, since many plants generally grow together, the Liverwort may cover quite large areas of ground. A detailed examination of a piece of the thallus shows that the upper surface is considerably darker green in colour than the lower, and is traversed by a purplish-coloured midrib. On the under surface numerous **rhizoids** are borne in the region of the midrib, and by these the plant is attached to the ground.

The internal structure of the thallus is simple, and is composed of polyhedral cells forming a uniform tissue called **parenchyma.** Unlike the plants which we have considered so far, which were predominantly made up of filaments, the thallus of the Liverwort is composed of layers of cells joined together in a honeycomb-like manner. We shall find that this form of tissue forms the basis of the tissue-organization of all land plants. The chloroplasts are restricted chiefly to the upper layers of cells, but starch grains occur in the cells throughout. These starch grains constitute the reserve food material resulting from Carbon assimilation. The layer of cells which covers the upper and lower surface of the thallus is called the **epidermis.** The rhizoids grow from the cells of the lower epidermis and are unicellular.

A Fungus mycelium is frequently, if not always, found in the cells of the lower part of the thallus, especially near the midrib, but is not normally found in the sporophyte. This Fungus is supposed to live symbiotically with the Liverwort. A similar endophytic Fungus is found in many other Hepaticae, but little is known about their biological relationships.

FIG. 372.—*Pellia epiphylla* growing on a shady bank. Half natural size.

Growth takes place by means of a single, large, apical cell, which lies at the base of a little depression between two lobes of the thallus. It cuts off segments both below and on its two sides. From the former the midrib is built up, whilst from the lateral segments the two lobes are developed. Since this lateral tissue grows more rapidly than the apex itself, it follows that the apical cell will always remain in a slight depression, thus being protected to some extent from damage. This growing apex is further protected by the development of hairs which secrete mucilage, and this prevents the apical cell from becoming desiccated.

The thallus branches **dichotomously,** and the beginning of this branching is marked by the longitudinal division of the apical cell into two, after which both apical cells continue to cut off segments in the same way as before.

Reproduction

Reproduction in *Pellia* is both sexual and asexual, but the two follow one another so that an immutable alternation of generations obtains.

As we have seen, the sporophyte is relatively small and lives parasitically upon the gametophyte. In *Pellia*, like all other Bryophyta, the thallus is the gametophyte, and upon it are borne the sex organs. They consist of **antheridia,** the male organs, and **archegonia,** the female organs.

The Antheridium

The antheridium arises from a single superficial cell which lies on the upper surface of the thallus immediately behind the growing point. It divides transversely forming a lower cell, which, after a few further divisions, forms the **stalk,** and an upper cell, which divides by a longitudinal septum into two, then into four and then into eight. By periclinal divisions there is formed an outer layer of cells enclosing a small central mass of cells. This layer constitutes the wall of the antheridium, whilst the central cells, after a considerable number of divisions, constitute **antherozoid mother cells.** Whilst development of this antheridium has been going on, growth has also taken place in the rest of the thallus so that the mature antheridium lies some distance behind the growing point, and a tissue has grown up completely enclosing it, except for a small opening at the top (Fig. 373).

From each antherozoid mother cell a single **antherozoid** is produced, which consists almost entirely of the nucleus together with two long flagella (Fig. 374). At the last division of the mother cells two plastid-like bodies are present, which are placed on each side of the nucleus and function as

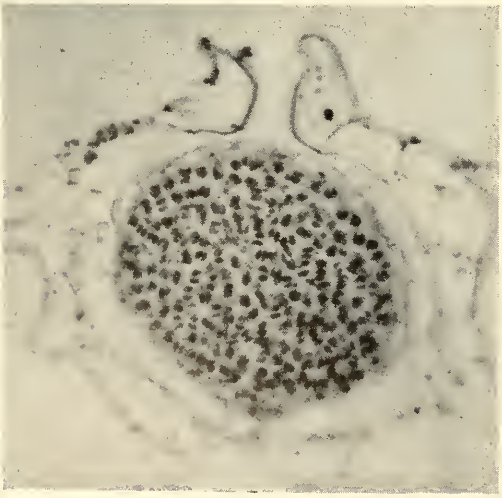

Fig. 373.—*Pellia epiphylla.* Vertical section of antheridium showing mature antherozoids.

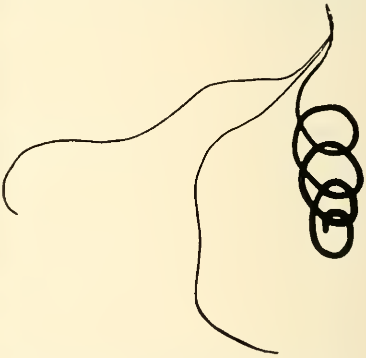

Fig. 374.—*Pellia epiphylla.* Mature antherozoid. (*After Showalter.*)

centrosomes, that is, they act as the poles of the spindles. During the formation of the antherozoids these bodies attach themselves to one end of the elongating nucleus and become **blepharoplasts,** which means that they develop the two flagella. The body of the antherozoid is tapered and spirally coiled, and the flagella are attached to the thinner end. The antherozoids are liberated by dissolution of the mother cells and the opening of the antheridial wall at the apex.

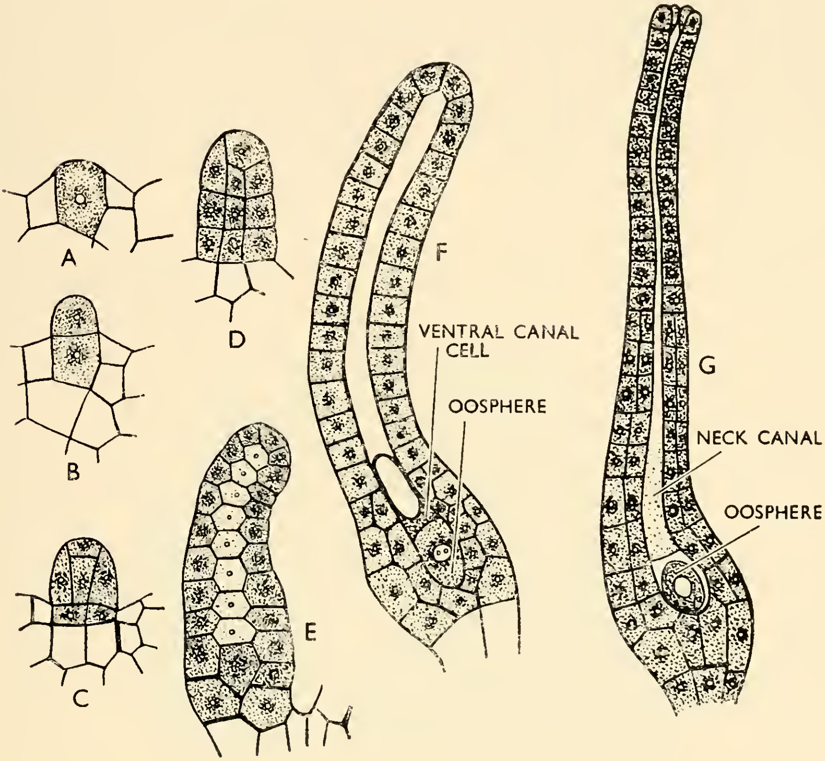

FIG. 375.—*Pellia epiphylla.* Development of the archegonium. A, Initial cell. B, C and D. Successive divisions forming the neck, neck canal cells, and ventral cell at the base of the neck canal. E, Differentiation of the ventral cell. F, Division of ventral cell into oosphere and ventral canal cell. G, Mature archegonium. The neck is open and the oosphere ready for fertilization. (*After Hofmeister.*)

THE ARCHEGONIUM

The archegonium arises from a single superficial cell of the thallus which enlarges and divides to cut off a **basal cell** (Fig. 375). From the upper cell the archegonium is produced. This cell divides by three vertical walls which form three peripheral cells, leaving a central cell in the middle. By a transverse wall a cap cell is then cut off so that the central cell becomes enclosed in a single layer of tissue. The peripheral cells now divide radially so that a ring of five or six cells is formed surrounding the central one. All the cells then divide transversely, differentiating the archegonium into two halves, the lower half forming what is known as the **venter,** and the upper forming the **neck.**

The central cell of the venter now divides unequally, forming a small, upper, **ventral canal cell** and a large lower cell, the **oosphere.** The peripheral cells of the venter divide tangentially to form a wall two cells thick. Meanwhile the neck elongates by the transverse division of its cells, forming thereby a tubular wall, one cell thick, which encloses a long **neck canal,** occupied at first by a row of thin-walled cells. Finally the cap cell divides into four.

The archegonia are produced in groups on the upper side of the thallus just behind the growing point (Fig. 376). They stand on the vertical face of a transverse ridge of tissue, facing towards the growing point of the thallus and lying almost horizontally. A delicate membrane grows from the top of the ridge, covering the archegonia as in a pocket. This cover is called the **involucre.**

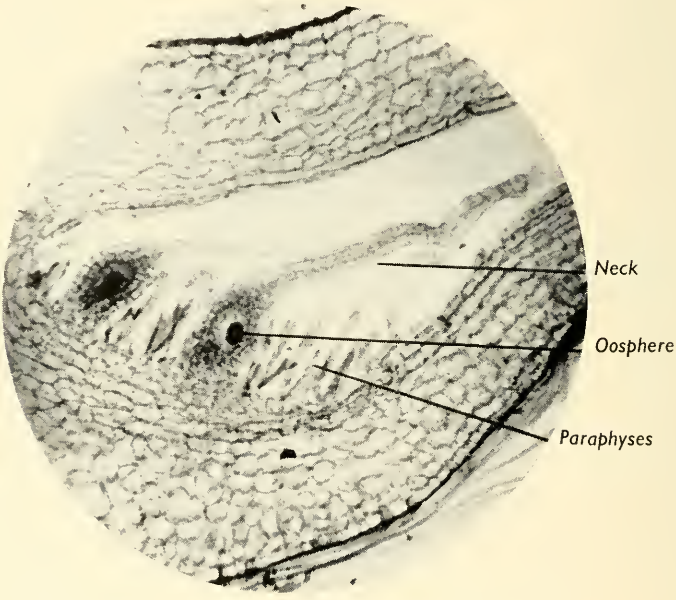

Fig. 376.—*Pellia epiphylla.* Section through involucral pocket showing archegonia covered by involucre.

In *Pellia* both male and female organs are borne on the same plant. When the archegonium is ready for fertilization mucilage is formed by the disorganization of the neck canal cells. This mucilage absorbs water, swells, and thus forces open the neck of the archegonium by separating the cap cells. At the same time the cells of the antheridium take up water, swell, and eventually burst the wall, liberating the antherozoids. These antherozoids make their way in the water film, which under damp conditions covers the thallus, and enter the neck of the archegonium, where they penetrate to the oosphere before losing their flagella. Fertilization is effected by the union of the nucleus of one antherozoid with that of the oosphere.

In all organisms which are fertilized by free-swimming gametes, some attractive force must operate to guide them towards the females. In the Bryophyta this is known to be the chemical attraction of sucrose, cane sugar, which diffuses from the mucilage at the open neck of the archegonium. This is an important example of **chemotropism,** which we shall discuss further in Vol. III.

THE SPOROGONIUM

After fertilization the **oospore** divides by a transverse wall into two cells, the lower of which plays no further part in development, whilst the upper cell continues to divide, first by a vertical wall and then by one at right angles to it. By further tangential cell divisions a layer of cells is formed which becomes the outer covering of the young embryo. Its further development consists in the formation of a capsule or **theca** at the top, and a stalk or **seta** below (Fig. 377). The capsule is formed from the upper part of the

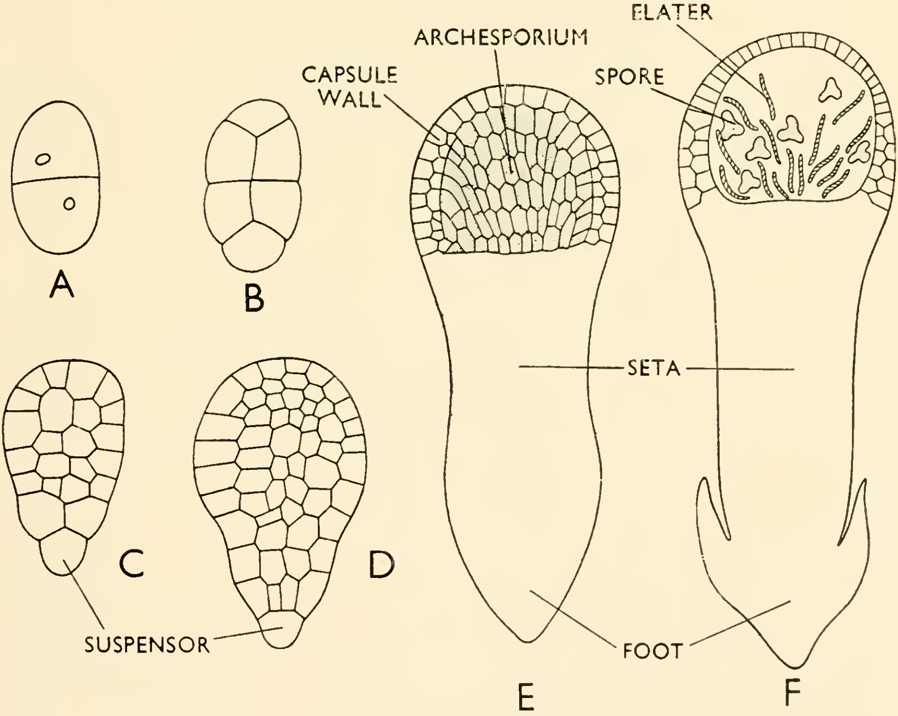

FIG. 377.—*Pellia epiphylla.* Development of sporogonium. A, First division of oospore. B, Further division of upper cell. C and D, Further stages in development. E, Differentiation of archesporium and capsule wall. F, Sporogonium at resting stage. (*After Hofmeister.*)

embryo, and consists of a single-layered wall surrounding a mass of cells, which is called the **archesporium,** from which the spores are formed. It is interesting to note that in the divisions of the archesporial cells centrosomes are present, a rare phenomenon in plants. The cells of the seta undergo repeated divisions but remain very short until the capsule is ripe. At its lower end the seta develops a conical **foot,** with a flange projecting upwards, in outline like a barbed arrow-head, by means of which it is firmly embedded in the thallus (Fig. 378).

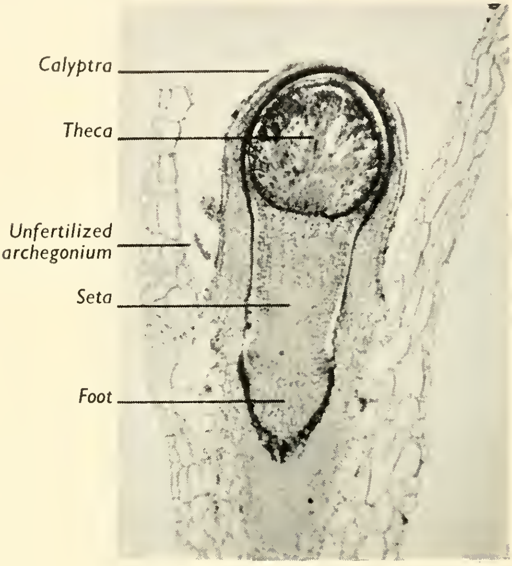

Fig. 378.—*Pellia epiphylla.* Longitudinal section of sporogonium enclosed in calyptra.

The wall of the capsule when mature becomes two cells thick, whilst from the archesporial tissue a large number of **spore mother cells** become differentiated. From each of these spore mother cells four spores are produced. During this process the spore mother cells become deeply four-lobed, with the lobes arranged pyramidally. The nucleus divides twice by meiosis, and one of the four nuclei passes into each of the lobes, which then separate and become differentiated into **spores.** Meanwhile a certain number of the archesporial cells, which have not become spore mother cells, grow considerably in length and ultimately form long, thin, doubly-pointed structures which are spirally thickened with ribs of cutin. These cells are termed **elaters.** When young they probably assist in transferring food material from the seta to the spores, but when the capsule is mature they assist in the dissemination of the spores.

It is important to realize that the whole of this development has been going on within the venter of the archegonium, which has therefore enlarged rapidly, keeping pace with the development of the sporogonium. For a long time this tissue, which is termed the **calyptra,** completely envelops the sporogonium. It is probable that the cells of the thallus contribute to this calyptra, for we find abortive archegonia carried up by its growth and lying on the surface of the calyptra, from which we conclude that rapid cell division has taken place in the tissues adjacent to the developing embryo. At the top of the calyptra the remains of the neck of the fertilized archegonium can still be made out.

Food for the developing sporogonium is obtained entirely from the thallus, and we find that the cells immediately below the foot of the seta become filled with starch. It is important to realize, however, that the foot never has any real tissue continuity with the cells of the thallus, and we can only assume that food material is absorbed by the foot from the surrounding cells, because the cells of the young seta also contain starch grains.

After its development the sporogonium remains dormant for several months, enclosed in the calyptra. By February it becomes sensitive to light and it normally elongates in March. The cells of the seta, already formed, elongate very rapidly by zones, from the base upwards, the basal zone elongating most. During elongation the seta bends upwards due to a positive reaction to light. As a result of this the calyptra is ruptured and remains as a torn membrane round the base of the stalk. During a period of not more than four days the seta grows to 2 or 3 in. long. It is quite slender, and is pure white and almost transparent in appearance, whilst the capsule at the top resembles a large black pin head. Whilst this elongation of the seta has been going on, germination of the spores has also taken place, and before they are shed from the capsule they may consist of several cells. Each cell contains chloroplasts and a nucleus, so that the spore is, in fact, a minute thallus (Fig. 379).

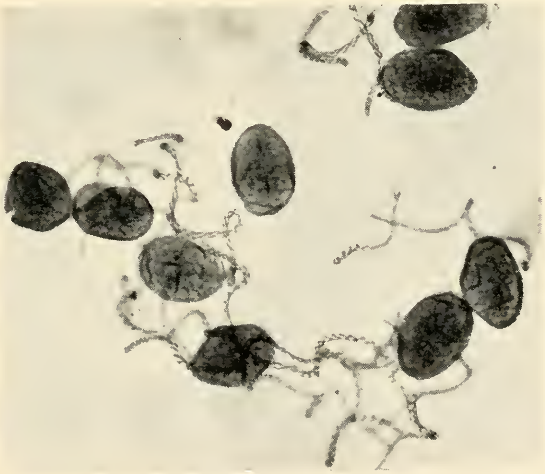

Fig. 379.—*Pellia epiphylla.* Multicellular spores and elaters after discharge from the sporogonium.

Under favourable conditions the capsule bursts by the splitting of the wall, forming four petal-like **valves** which spread out horizontally. By this means the spores are liberated and the separation of the spores from one another is assisted by the eIaters. The elaters are **hygroscopic,** that is to say, they expand and contract according to the degree of atmospheric humidity, during which process they twist and turn rapidly, and it will be realized that by this means they stir up the spores and separate them. The elaters are arranged in radiating lines from a solid tuft at the base of the theca, and when all the spores are shed this tuft of elaters, in the centre of the four spreading valves of the wall, produces the semblance of a minute flower.

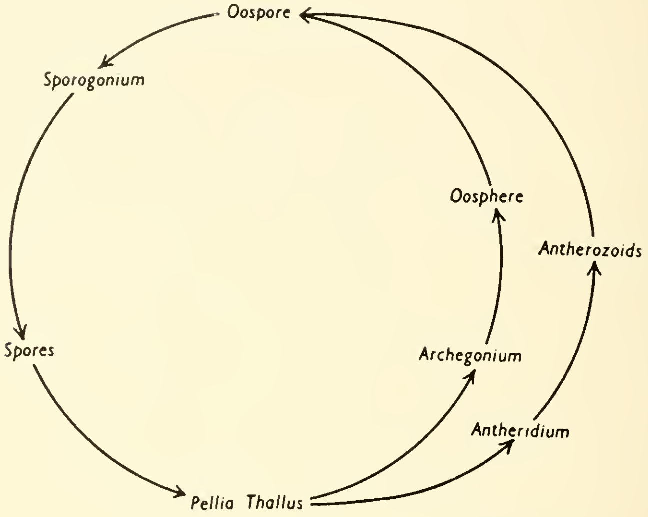

FIG. 380.—Life-cycle of *Pellia epiphylla.*

On liberation the multicellular spore begins to grow at once, for, like other spores containing chlorophyll, it has no resting period. A cell at one end of the spore becomes the apical cell, the others form the ordinary cells of the thallus, and the various parts of the *Pellia* thallus soon become differentiated.

ALTERNATION OF GENERATIONS

From our study of the life history of *Pellia* we see that the sexual and asexual reproductive phases are very closely connected ; far more closely than they are in a type like *Dictyota* or *Polysiphonia*. In either of these algal types the asexual plant possesses an independent life, whereas in *Pellia* the sporophyte lives in and upon the gametophyte.

The life history of *Pellia* may be summarized by the above diagram (Fig. 380).

Marchantiales

The Marchantiales are Hepaticae in which the thallus is composed of several distinct layers of tissue, of which the uppermost, the chlorophyll-bearing layer, nearly always encloses air chambers, which have communication with the exterior through pores. The rhizoids are of two kinds, smooth and tuberculate. The sex organs are generally united in receptacles often borne on long-stalked antheridiophores and archegoniophores respectively. The order includes relatively few British genera, though some of the species are among the commonest Liverworts.

We shall consider as our example of this order *Marchantia polymorpha.*

Marchantia polymorpha

Our second example of the Hepaticae, *Marchantia polymorpha*, is more complicated than *Pellia* both in the structure of the thallus and also in the sexual reproductive organs. The general morphology of the thallus of the two plants is much the same (Fig. 381). It is flat, dichotomously branched, possesses a central midrib and develops rhizoids on the lower surface in the same way as in *Pellia*. There is, however, this considerable difference, that there is no special apical cell, as in *Pellia*, but a group of meristematic cells at the apex.

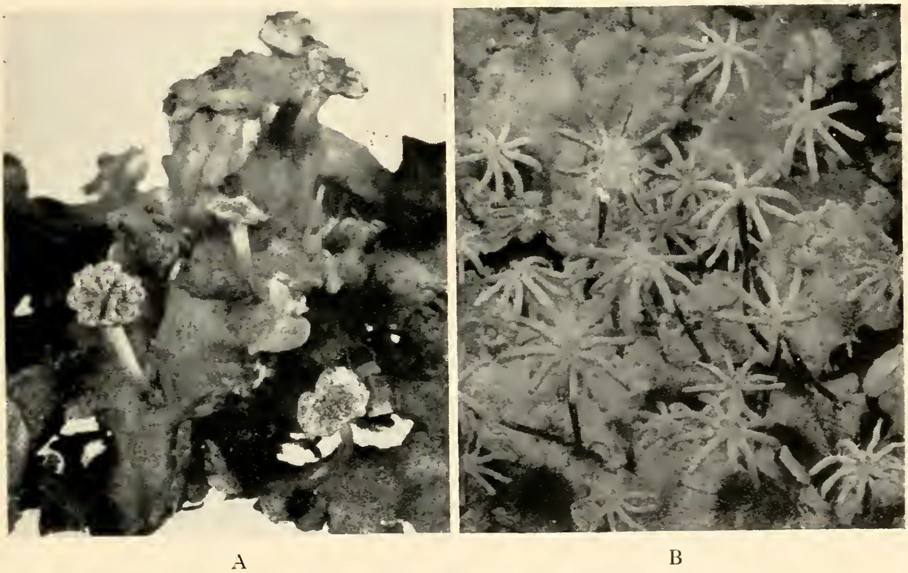

Fig. 381.—*Marchantia polymorpha.* Habit photographs. A, Male thallus. B, Female thallus about life size.

When we come to examine the internal anatomy of this thallus we find that there is considerably greater differentiation of tissues. In *Pellia* the thallus was composed of a more or less uniform parenchyma ; in *Marchantia* we can distinguish a number of distinct layers (Fig. 382). Starting from the upper surface there is first of all a single layer of **epidermal cells.** Embedded in this are special **ventilating pores** which allow the passage of gases through the epidermis. These pores are surrounded by four rows of four cells, the rows forming rings one above the other, leaving an aperture in the centre.

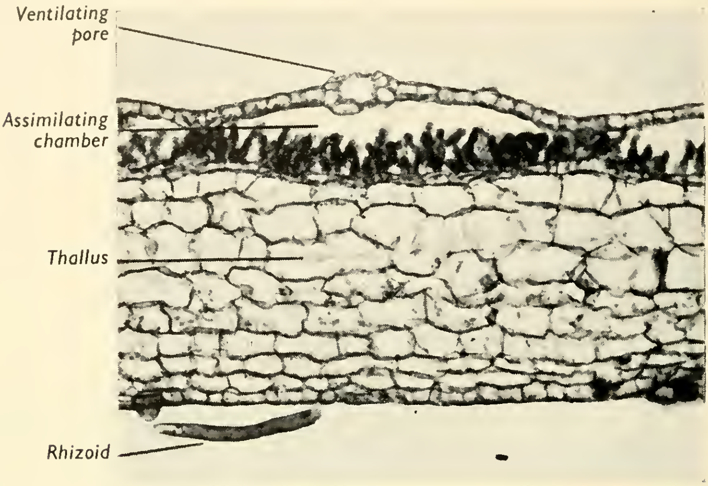

Fig. 382.—*Marchantia polymorpha.* Vertical section showing structure of thallas.

Thus the pore wall lies half above and half below the epidermis. Below the epidermis there are a number of chambers, within which are short, sometimes branched, filaments of cells, which develop from the flat base of the chamber, which is composed of cells similar in shape to those of the epidermis. The chambers, as seen from above, are diamond-shaped areas and are bounded by walls of three or four cells in height, which unite the epidermis above with the parenchyma below. All these cells, and particularly the filaments within the chambers, are dark green in colour, due to the presence of numerous ovoid chloroplasts. Each chamber lies directly under one of the ventilating pores, and there is no doubt that the green filaments are the principal centres of photosynthesis in the thallus.

The lower layers of the thallus are made up of relatively large parenchyma cells similar to those in the thallus of *Pellia*, among which are a number of large **mucilage cells.** The lower surface is covered with an epidermis composed of cells similar to those of the upper epidermis, and from these cells two types of outgrowths arise. Firstly, there are the **rhizoids,** which are unicellular and contain very little protoplasm, and, secondly, a number of multicellular scales or **amphigastria,** which form two overlapping rows, one on each side of the midrib. The amphigastria no doubt serve to retain moisture below the thallus which the rhizoids can absorb. These rhizoids, like those in other members of the Marchantiales, are of two kinds ; one set are smooth-walled, the others show a large number of minute thickenings or **tubercles** which project from the walls into the lumen of the rhizoid cells. The smooth rhizoids emerge from behind the amphigastria and penetrate the soil. The tuberculate rhizoids lie parallel to the underside of the thallus and form a system of conducting strands leading forwards to the growing point, where water is readily absorbed. It may be correlated with this that *Marchantia* can grow in much drier places than *Pellia* can. Damaged rhizoids may be regenerated, secondary and even tertiary rhizoids proliferating within the primary one.

VEGETATIVE REPRODUCTION

There are two methods of vegetative reproduction in *Marchantia*. The first depends upon the ageing of the vegetative cells. It appears that the cells of the thallus only live for a month or two, and as new cells develop at the apices of the branches those further back die and eventually disorganize. In this way the individual branches become separated, and each continues life independently.

The second method of vegetative reproduction is by means of **gemmae.** These gemmae are lens-shaped masses of cells, which when detached develop into new plants. They are developed in the base of small cup-shaped organs termed **cupules,** which are produced along the midrib (Fig. 383). The gemmae arise from a superficial cell which divides into two. The upper cell enlarges and divides further to produce a group of cells with an indentation at each end which marks the presence of a growing point. When mature the gemma is liberated by the disorganization of the stalk formed by the basal cell (Fig. 384). On its liberation the gemma develops into a fresh thallus, growing from both ends simultaneously. Gemma formation usually

FIG. 383.—*Marchantia polymorpha*. Vertical section through gemma cup containing gemmae.

takes place during the autumn and spring, and affords a very rapid and successful means of dispersal during the growing season.

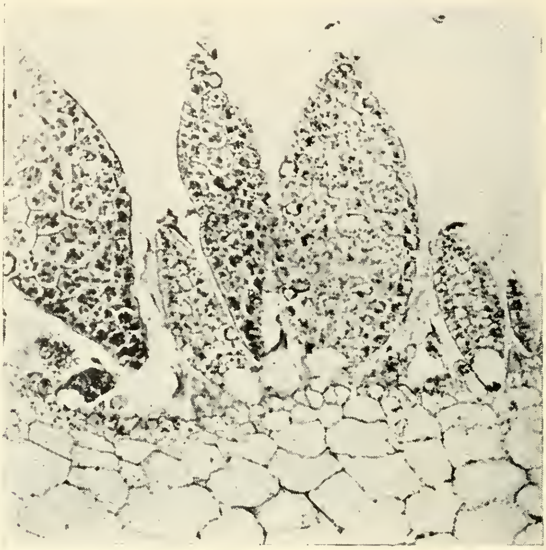

Fig. 384.—*Marchantia polymorpha.* Development of gemmae showing stalk formed by basal cells.

Sexual Reproduction

Marchantia polymorpha is dioecious, that is to say, that the male and female reproductive organs are borne on different plants. The sex organs are generally produced during the summer, and differ markedly from those of *Pellia.* Instead of being immersed within the tissues of the thallus, the sex organs are elevated upon special branch structures, termed respectively the **antheridiophore,** which bears the male organs, and the **archegoniophore,** which bears the female organs. Both structures are developed at the growing apex and form a direct continuation of the midrib, but they grow vertically upwards through the apical indentation in the thallus until they are as much as 3 cm. in height. In general structure these organs resemble the thallus, and we must regard them as branches of the thallus, borne on the end of stalks, rather than as purely reproductive bodies.

The Antheridiophore

The antheridiophore consists of a stalk bearing at its apex a disc-shaped cap (Fig. 385). In transverse section this stalk is seen to consist of a narrow thallus branch, the margins of which are curled downwards and inwards until they almost meet below the midrib, thus forming two vertical channels running up the stalk (Fig. 386).

The disc is made up of eight separate lobes, the indentations between

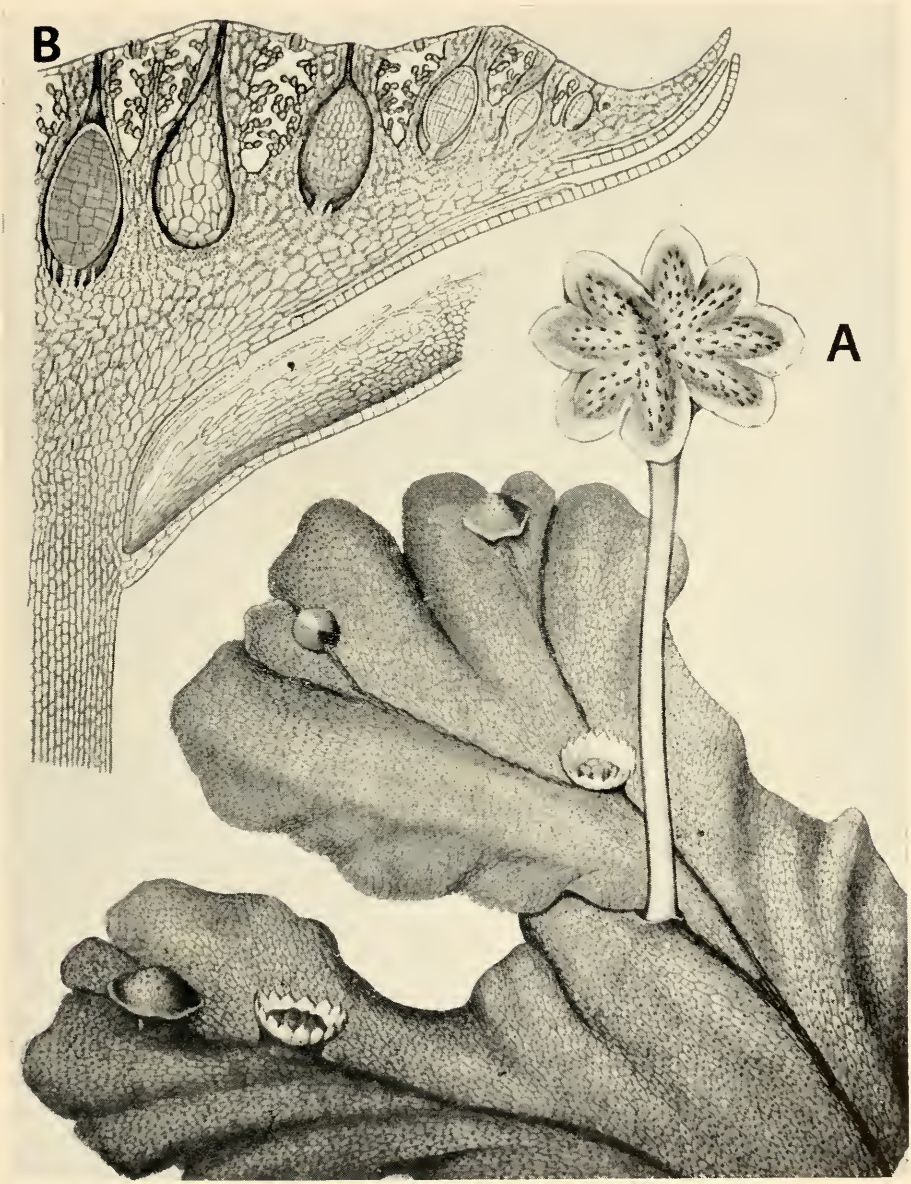

Fig. 385.—*Marchantia polymorpha.* A, Male plant with antheridiophore and gemma cups. B, Vertical section through part of antheridiophore showing centrifugal development of antheridia immersed in thallus tissue. (*From Kny.*)

which represent the apices of a corresponding number of branches. This disc has all the features of the anatomical structure of the thallus. There is the same type of epidermis with its ventilating pores and the same large chambers containing assimilatory filaments; amphigastria are present, and rhizoids are given off from the lower surface and pass downwards through the channels of the stalk. The antheridia are embedded in cavities sunk in the tissues between the chambers and lined by a layer of cells whose walls are often deep purple in colour. Each cavity is oval in shape, has a tubular opening upwards, and contains a single large **antheridium,** which is attached by a short stalk at the base. The development of the antheridium is essentially similar to that in *Pellia*, and the **antherozoids** when mature are liberated by the bursting of the antheridium and are extruded out of the chamber in a drop of milky liquid (Fig. 387). They are subsequently transferred to the archegoniophore, possibly through the agency of dew or rain falling on the upper surface of the antheridiophore. Mites have been found in the chambers of the archegoniophore, bearing antherozoids on their bodies,

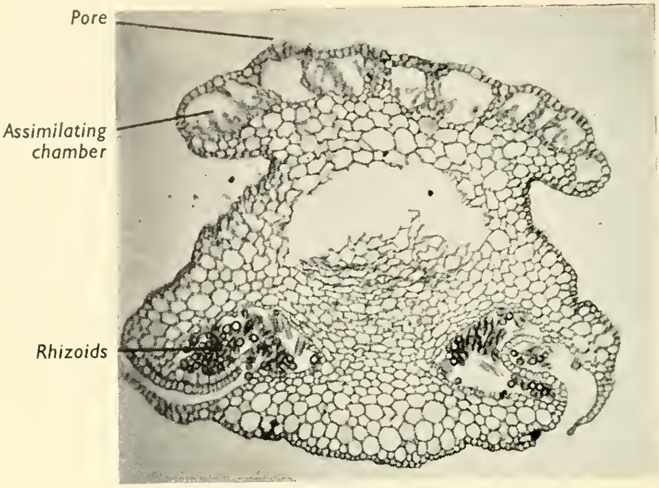

Fig. 386.—*Marchantia polymorpha*. Antheridiophore, transverse section of stalk showing thalloid structure.

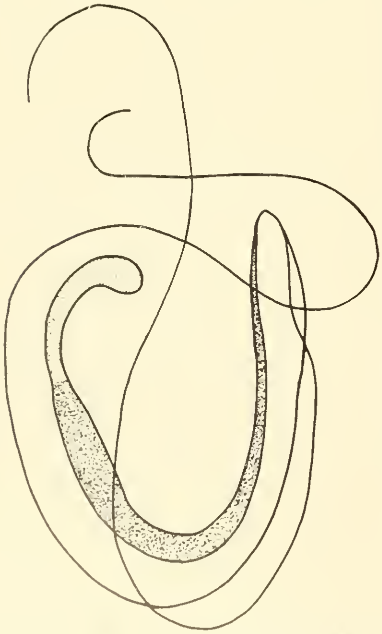

Fig. 387.—*Marchantia polymorpha*. Mature antherozoid. (*After Woodburn.*)

and since sucrose is secreted by both antheridia and archegonia it has been suggested that a form of " insect pollination " may occur in *Marchantia.*

THE ARCHEGONIOPHORE

The archegoniophore is similar in general structure to the antheridiophore. It is made up of a stalk, which is generally longer than that of the antheridiophore, and a terminal disc, which is also branch-like (Fig. 388). The growing apices of these branches, however, turn downwards and inwards towards the stalk so that their positions are marked by deep indentations in the disc. The tissue between these growing points projects as long finger-shaped processes, like the ribs of an umbrella. The **archegonia** are formed in small triangular patches near each of the down-turned apices. Each patch is surrounded by an **involucral membrane,** which is developed from the edges of the ribs and hangs down vertically to protect the developing archegonia. Some twelve to sixteen archegonia are produced in each of these enclosures, and develop in succession from the outside inwards (Fig. 389). Their development is more or less similar to that in *Pellia*, and it is unnecessary for us to consider it in detail. There is, however, one difference, that each archegonium is surrounded by an individual collar of cells called the **perianth.**

The stalk of the archegoniophore is provided with the same two longitudinal grooves that we have noted were present in the antheridiophore, and it has been suggested that the function of these grooves is to provide a water channel in which the antherozoids may swim down the antheridiophore and up the archegoniophore to reach the archegonia. We do not really know precisely how the male gametes find their way to the archegonia, but from the fact that fertilization of the **oosphere** is effected we know that they must do so. When we consider not only the distance between the sex organs and the ground but also the fact that the sexes are on different plants, we can clearly see the difficulties in the way of fertilization by a microscopic antherozoid, and the advantages of having a good method of vegetative propagation.

The result of fertilization is the development of a **sporogonium** in a way similar to that in *Pellia.* The **oospore** divides into eight cells, four of which form the **foot** and the **seta,** whilst the upper four cells give rise to the **capsule.** The details of this development are sufficiently similar to those in *Pellia* for it to be unnecessary for us to consider it in detail. It is interesting to note, however, that during the development of the sporogonium the stalk of the archegoniophore may elongate considerably, but not the stalk of the sporogonium, as in *Pellia*, whence we are forced to conclude that the reaction produced as a result of fertilization is not restricted solely to the embryo, but extends also to the tissues surrounding it. As the sporogonium hangs downwards the elongation of its stalk would merely carry the spore capsule down to the ground (Fig. 390).

When mature the sporogonium becomes yellow in colour and splits open by from four to six valves. The **spores** with their accompanying **elaters** are shed, and, due to the elevation of the sporogonium on the archegoniophore, may possibly be better distributed than is the case in *Pellia*. The elaters function like the annulus of a Fern sporangium (p. 491) by means of an

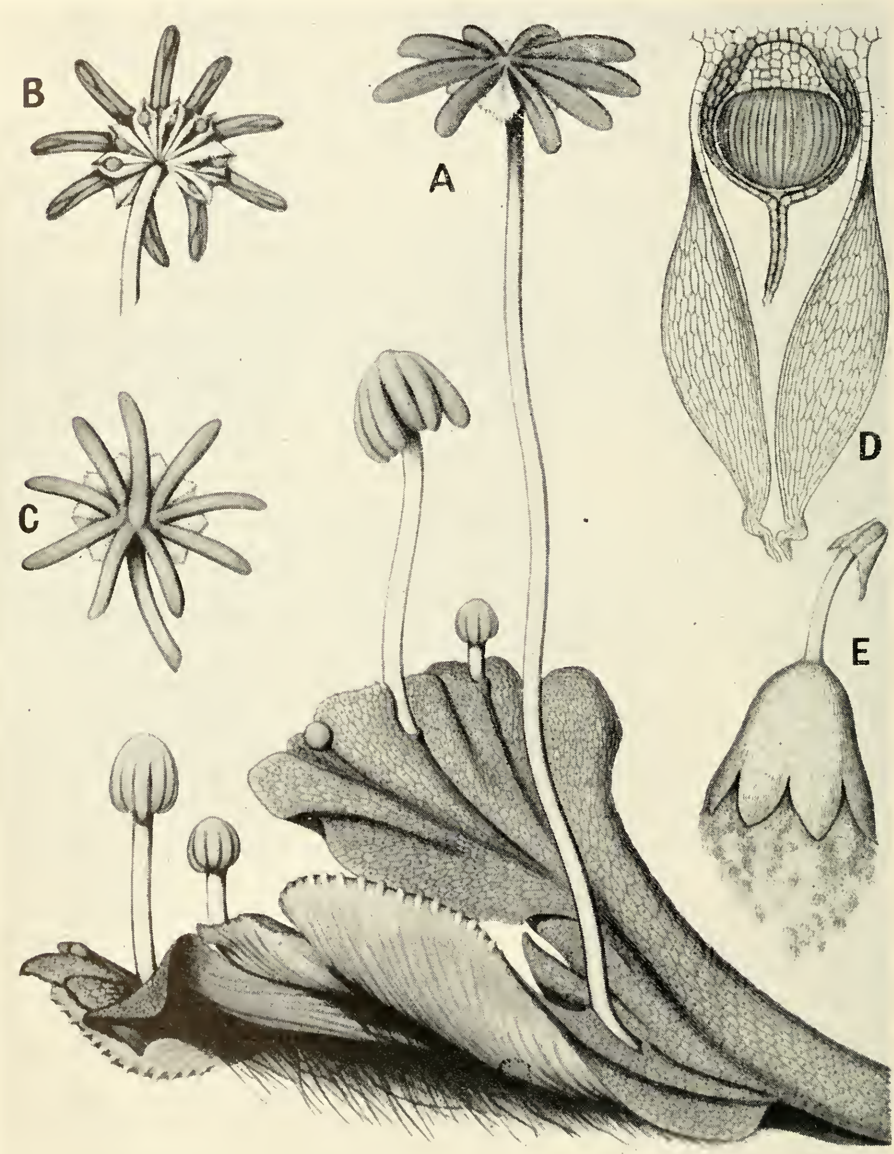

Fig. 388.—*Marchantia polymorpha*. A, Female plant with archegoniophores in various stages of development. B, Under surface of archegoniophore showing sporogonia enclosed in involucres. C, Upper surface of archegoniophore showing arrangement of lobes between which are the involucres. D, Young sporogonium enclosed in archegonium between involucral flaps. E, Dehiscence of sporogonium. (*From Kny.*)

internal water tension set up as the elaters dry. This causes twisting, which is violently released when the water tension breaks down, causing the elater to spring back explosively into its normal form, thus scattering the spores. On reaching the ground the spores germinate immediately to produce a tiny

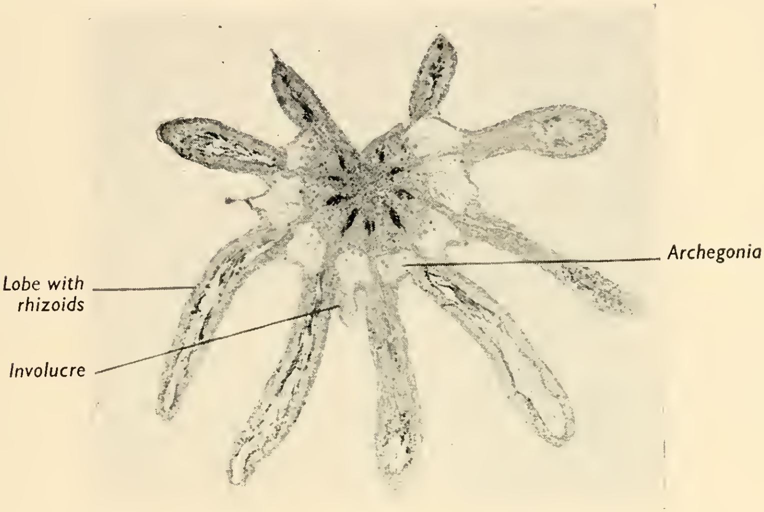

Fig. 389.—*Marchantia polymorpha.* Horizontal section through archegoniophore, showing rhizoid channels in lobes and involucres containing groups of archegonia.

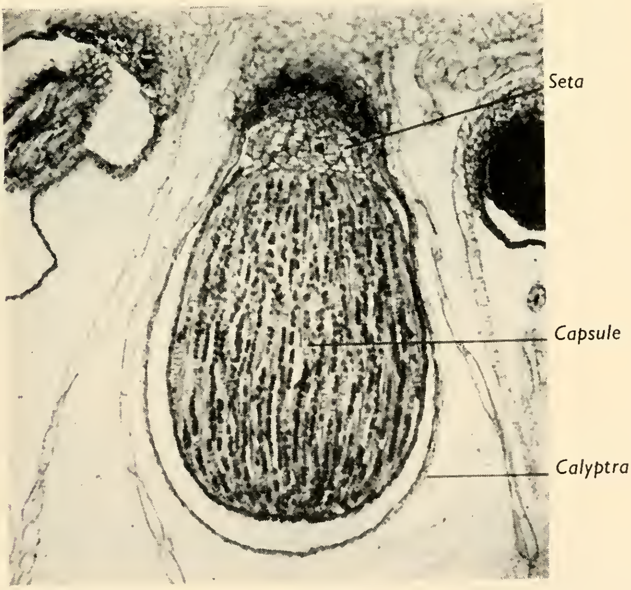

Fig. 390.—*Marchantia polymorpha.* Young sporogonium showing development of spores and elaters from archesporium.

filament, from which a fresh *Marchantia* thallus is produced. Since the sex organs are developed on different plants it follows that the spores must be of two kinds. As we shall see later in our consideration of the Laws of Inheritance it is probable that male and female producing spores arise in equal numbers, but female plants are commoner than males.

ALTERNATION OF GENERATIONS

The life history of *Marchantia*, it will be seen, is similar to that of *Pellia*. Apart from the purely asexual production of gemmae there is a definite alternation between a gametophyte, the thallus on which the gametes are borne, and a sporophyte in which the spores are produced. In so far as the sporophyte develops within the archegonium and derives its nourishment therefrom there is little difference in the two examples. In fact a relatively small and parasitic sporophyte is characteristic of the whole of the Bryophyta, and it is not until we pass to the Pteridophyta that we shall find any change in its importance.

The life-cycle of *Marchantia* may be illustrated graphically by the following diagram (Fig. 391) :—

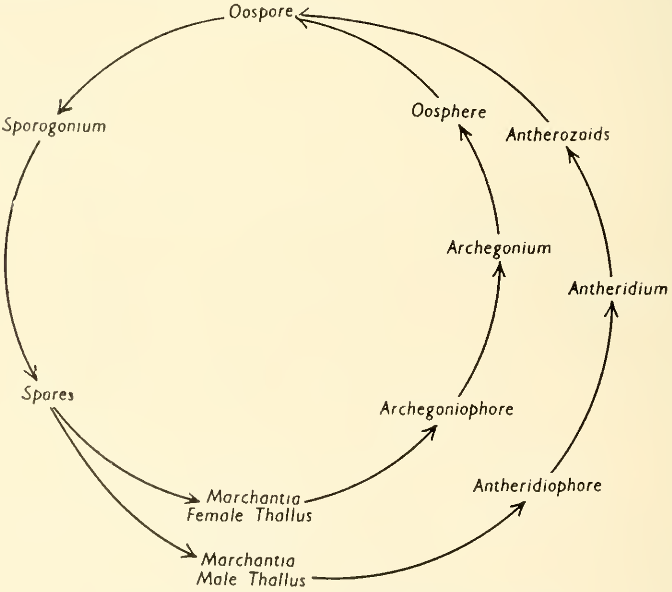

FIG. 391.—Life-cycle of *Marchantia polymorpha*.

Anthocerotales

The Anthocerotales are Hepaticae in which the thallus is simple and undifferentiated in structure. The sporogonia are remarkable for their continued growth from a basal meristem. They are long and narrow with no distinction between capsule and seta, and they mature progressively from the apex downwards.

This very small order, which embraces only four genera, is important because of its isolated position among Bryophyta and because some botanists have seen in it a presage of the independent sporophyte which is characteristic of the Pteridophyta. The plants are all small thalloid types, living under very moist and shady conditions, and none of them is common. *Anthoceros* itself is the best known, and we will confine our remarks to it.

Anthoceros laevis

There are six species of *Anthoceros* in Britain, all rather similar, among which our species may stand as a type. It is widely distributed, especially in the west and north, but is nowhere common, though when found it may be locally very abundant. It grows on moist soil, on the sides of shady ditches or in moist hollows among rocks. The plant is the gametophyte and forms a small, dark-green, translucent thallus, 5 to 15 mm. across, divided into smooth, broad lobes, with the margins **crenate,** that is to say, formed of small rounded lobe-segments (Fig. 392). The sporogonia are long, delicate, green structures, like blades of grass, which grow in clusters from the back of the thallus, usually in the winter months. The species is dioecious, male and female sex organs being on separate plants.

FIG. 392.—*Anthoceros laevis.* Plants with mature sporogonia. Natural size.

Anthoceros is able to absorb water all over the surface of both gametophyte and sporophyte. The water rises over the edge of the thallus on to the dorsal surface and thence to the sporogonium. A slow conduction takes place internally from the foot of the sporogonium, but it is of minor importance compared with the external conduction.

Structure of the Thallus

The tissues of the thallus are very simple and are parenchymatous throughout, the upper and lower surfaces being formed of smaller cells, but not cuticularized or otherwise distinguished beyond the fact that the plastids in the upper surface layer occupy nearly the whole cell. Every cell of the thallus contains one large irregularly shaped chloroplast containing one **pyrenoid** (Fig. 393), with numerous small starch grains. The pyrenoid is peculiar to this genus, and is the only case of its occurrence outside the Algae. The division of the chloroplast precedes cell division. The two plastids move to opposite sides of the nucleus, where they behave as centrosomes, the spindle fibres running between them across the nucleus. The thallus is six to eight cells thick, the central layers having only small plastids and no intercellular spaces. Smooth-walled unicellular **rhizoids** are formed below the thallus.

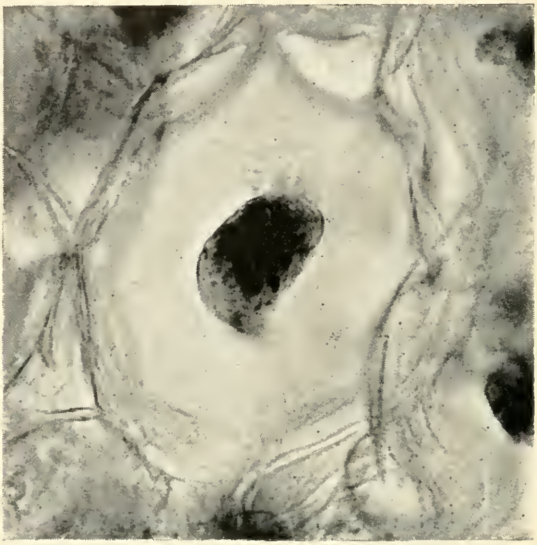

Fig. 393.—*Anthoceros laevis.* Cell of thallus showing the single large chloroplast containing stained starch grains.

In its early stages the thallus grows by a single apical cell, but in mature specimens there may be many, scattered along the margin and separated from each other by small projections, the **middle lobes,** which later develop into the characteristic crenulations of the margin.

At certain places the superficial cells of the lower surface separate from each other, leaving intercellular slits filled with mucilage, which oozes out and holds water between thallus and soil. These **slime pits** deepen and invade the interior tissues, forming rounded cavities filled with mucilage, which are often inhabited by colonies of the Cyanophycean Alga, *Nostoc.*

Neighbouring cells grow out among the Algae in the form of filaments. Stomata of the same type as those found on the sporophyte, with two bean-shaped guard cells and an open slit, occur on the lower, and also in places on the upper, side of the thallus. As there is no organized epidermis, gaseous diffusion into the tissues is not limited to these stomata, which probably only serve as outlets to the intercellular slime passages, which permeate the inner tissues. Their presence and their structure, which resembles closely that found in higher plants, speak strongly for the view that *Anthoceros* is a morphologically reduced rather than an advancing type.

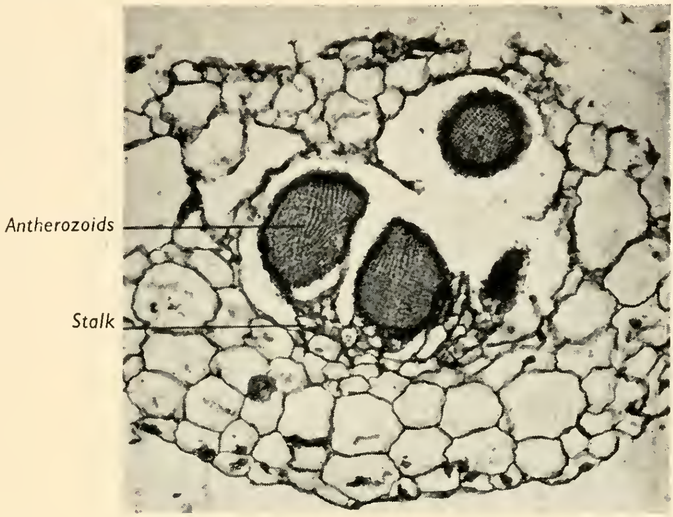

FIG. 394.—*Anthoceros laevis*. Section through an antheridial cavity containing antheridia.

In the sporophyte the stomata open into internal air spaces and are apparently normal in function.

The algal affinity suggested by the presence of pyrenoids in *Anthoceros* is borne out by the production of vegetative reproductive bodies, or **gemmae,** which are produced on short stalks on the upper surface of the thallus in *A. glandulosus*. Occasionally marginal **tubers** may be formed, which can survive periods of drought. They are developed from modified thallus lobes and store fat and protein; when detached they function as organs of vegetative propagation.

THE ANTHERIDIUM

The development of the **antheridia** is endogenous. A surface cell divides horizontally, the inner half forming a group of antheridia, and the upper half forming a roof over them. The inner cell divides again twice, vertically, each of the four cells thus formed usually developing into an antheridium, though sometimes only two or three develop (Fig. 394). The roof cell meanwhile divides and grows while the surrounding cells shrink away, so that the antheridia lie in a cavity and are only exposed, when mature, by the breaking open of the roof. The structure of the individual antheridium is closely similar to that in other Liverworts, but this endogenous formation is unique and has led to some controversy as to whether the male organs in this plant are really homologous with antheridia elsewhere. The general opinion is in favour of their homology and regards their present position as derived from a superficial position in former times.

The antherozoids are like those of other Hepaticae.

The Archegonium

The **archegonia** differ from those of other Liverworts, and from those of the Ferns in several particulars (Fig. 395). They originate from a single superficial cell. This divides vertically to form three peripheral cells and a primary central cell. The peripheral cells become the archegonial wall, but as they are completely sunk in the thallus tissue their further development is indistinguishable from that of the neighbouring cells. The primary central cell now divides horizontally. The lower portion divides again to form the **oosphere** and the **ventral canal cell,** while the upper portion, or cover cell, forms the six **neck canal cells** and the four cells that form a group or mouth at the top of the neck. These latter project above the general thallus surface. All the cells in the neck above the oosphere gelatinize and disappear, leaving a clear opening down to it.

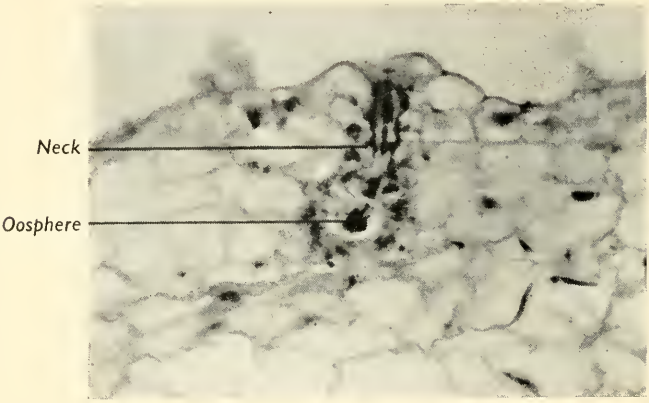

Fig. 395.—*Anthoceros laevis.* Longitudinal section of thallus through an archegonium.

The Sporogonium

The zygote divides into four tiers of four cells each. From the uppermost the **sporogonium** proper develops, while the lower three make up the **foot.** Periclinal divisions of the four top cells cut off an inner group of four, which become the **columella.** They represent the **endothecium** of the Moss capsule, but in this case, though not in the Mosses, the spore layer is formed from the outer zone of cells, the **amphithecium.** When fully developed the sporogonium consists of a slender cylindrical upgrowth, very like the cotyledon of an onion seedling. The sporogonium shows, in transverse section (Fig. 396), an epidermis with well-developed cuticle and **stomata**; three to four layers of amphithecial cells and then a layer of **spores** grouped in tetrads round the central columella, which is usually shrunken to small dimensions. Owing to their close grouping in tetrads each spore is pyramidal in shape and has a yellowish, warted wall. Among the spores are short chains of one to four small cells of irregular shape which are called **pseudo-elaters** and probably have a similar function to true elaters.

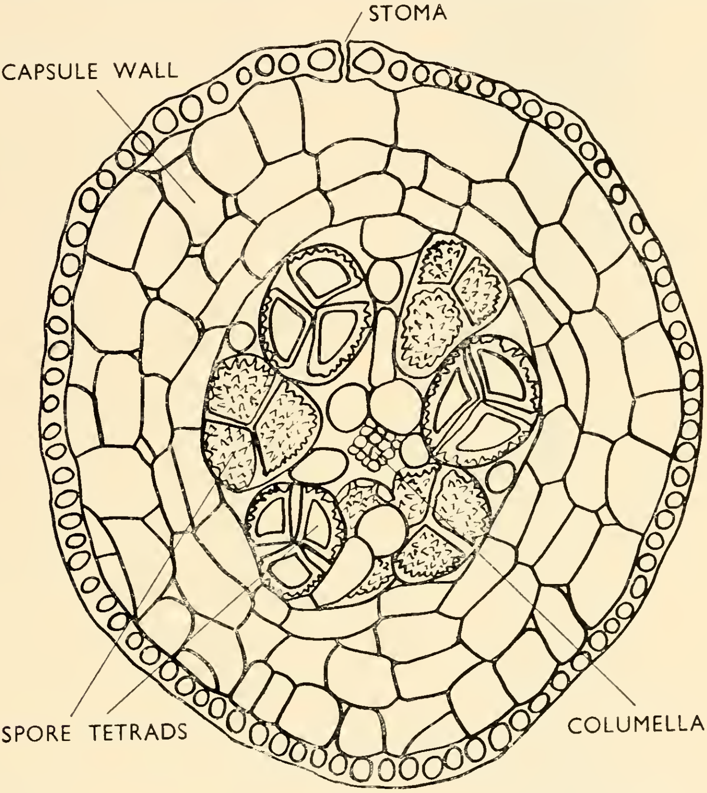

Fig. 396.—*Anthoceros laevis.* Transverse section through middle part of sporogonium. (*After Goebel.*)

In longitudinal section (Fig. 397) the spore layer is seen to extend over the top of the columella like a saddle, a feature shared only with *Sphagnum.* At the base of the sporogonium the lowest portion of the columella and its surrounding cells remain **meristematic**, and by intercalary growth in this region the sporogonium gradually elongates to a length of 2 or 3 cm. In any one sporogonium, therefore, all stages of development may be seen.

The apex may have already dehisced longitudinally by the splitting of the amphithecium into two parts, and have liberated its spores, while in the lower portion all stages in the formation of the spores are still to be seen. The valves twist hygroscopically after dehiscence and may thus assist spore dispersal. The basal portion of the sporogonium is enveloped by a tubular upgrowth of the archegonial wall, forming a **calyptra.** The growth and dehiscence of the sporogonium continue as long as the gametophyte lives, which is in marked contrast with the short-lived sporophytes of other Liverworts.

The lowest cells of the embryo also divide, though less vigorously, to form a rounded mass, the **foot,** the outer cells of which form short **rhizoids,** penetrating the tissues of the gametophyte, from which they absorb nutriment. This formation of rhizoids from an actively growing foot has suggested the speculation that the sporophyte might in this way become independent, the foot penetrating the thin tissue of the thallus to become a root in the soil and thus establish the sporophyte as a self-supporting plant. There is no evidence, however, that this interesting possibility ever became a fact. Indeed a similar development of rhizoids from the sporogonium is known in some Mosses where there is no likelihood of the sporogonium achieving independence. Moreover in the Fern embryo, where there is an actual root, there is also a foot, which is quite a distinct structure.

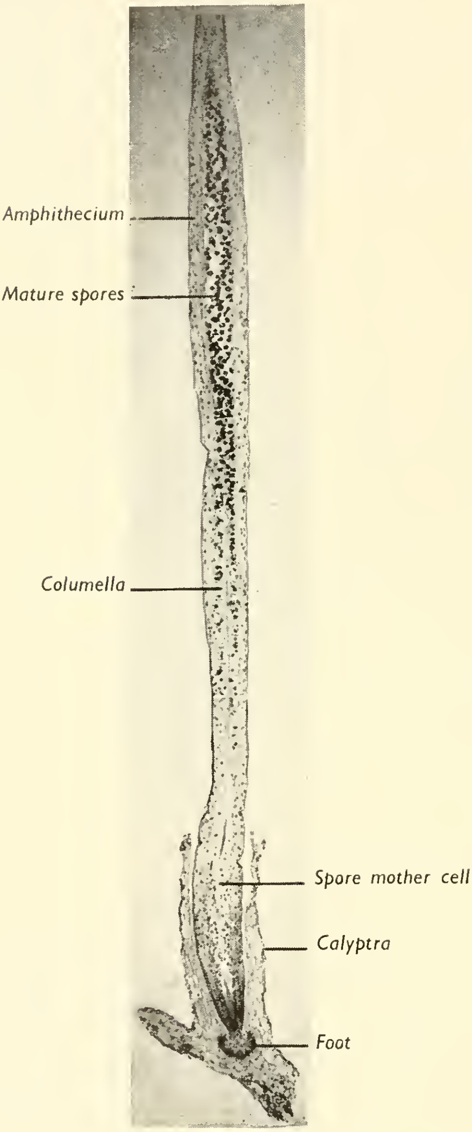

FIG. 397.—*Anthoceros laevis.* Longitudinal section through sporogonium and calyptra.

CHAPTER XII

THE BRYOPHYTA: MUSCI, THE MOSSES

THE Musci are Bryophyta in which the body is characteristically divided into stem and leaves. The former may be erect or prostrate, and the leaves may be very small and little more than short green outgrowths, or they may be flat and expanded, like miniatures of the leaves of higher plants. In the anatomy of the stem there is a certain amount of tissue differentiation, but no true vascular system is developed. Cellulose is rare in the cell walls, which are composed chiefly of hemicelluloses and pentosanes. The sex organs are either produced on separate plants or on separate branches, or even on the same branch of the same individual, immersed in a group of leaves at the apex of the branch, and this structure is sometimes referred to as the "flower." As a result of fertilization a sporophyte is developed which consists of a stalk and a capsule in which the spores are enclosed. This capsule is often highly specialized. It possesses stomata and chloroplasts, which distinguish it from the corresponding structure in most of the Hepaticae.

The spores on germination give rise to a filamentous structure, termed a **protonema,** somewhat resembling in appearance the thallus of *Vaucheria*, and from it the numerous leafy shoots arise which compose the mature Moss plant.

The fossil history of the Mosses goes back as far as the Carboniferous times. In the Mesozoic there are only very scanty remains, but in the lower Tertiary a number of peculiar forms have been found embedded in amber of Eocene age. In the Pliocene there are remains of forms still living at the present day.

The Musci are divided into three orders of which we shall consider examples of two :—

1. **Bryales** (*e.g.*, *Mnium*, *Polytrichum*).
2. **Sphagnales** (*e.g.*, *Sphagnum*).

Bryales

The Bryales is by far the largest order of the Mosses and includes nearly all the common families. They are characterized by the fact that both the columella and the spores are developed from the inner tissues of the sporogonium. The spore sac is separated from the wall of the capsule by an air space. The capsule dehisces either by a lid or irregularly.

We shall consider two examples of this group, *Mnium hornum* and *Polytrichum commune*.

Mnium hornum is relatively simple in structure and has been selected in preference to the well-known type *Funaria hygrometrica*, which it resembles, owing to the fact that in most parts of the country it is more easily obtained in the quantities necessary for class material. The description of *Mnium*, however, covers in all essential features the characteristics of *Funaria*. *Polytrichum commune* is a rather specialized Moss showing considerably more elaborate structure than that of *Mnium*.

Mnium hornum

This common Moss is found growing in large tufts in woods, especially Beech woods, and on shady banks. It is 2 to 3 in. in height, bright green in colour, and consists of a brownish-green stem covered with prominent leaves which are developed spirally (Figs. 398 and 399). The reproductive organs are produced on separate plants at the apices of the branches and are surrounded by an **involucre** of larger leaves. They appear during May and June, and the female plants frequently bear archegonia and old capsules at the same time. The male flowers are yellowish-red, and more conspicuous than the female, as the involucral leaves stand out in a circle round the cluster of antheridia.

FIG. 398.—*Mnium hornum*. Leafy plant bearing sporogonia. Natural size.

The stem tissues show a certain amount of differentiation, and it is possible to distinguish a central **axial cylinder**, about one-fifth of the diameter of the stem, composed of narrow, much-elongated, thin-walled

FIG. 399.—*Mnium hornum.* Antheridial heads on gametophyte showing the involucre of large leaves. Enlarged.

cells, known as **hydroids** (Fig. 400), and an outer tissue termed the **cortex,** composed of wider cells, with brownish-coloured walls, containing some starch grains and chloroplasts. The innermost layer of the cortex may be distinguished by its greater resistance to the swelling action of sulphuric acid, and although it is not justifiable to regard this layer as comparable with an endodermis (see p. 457), we realize that already in these simple

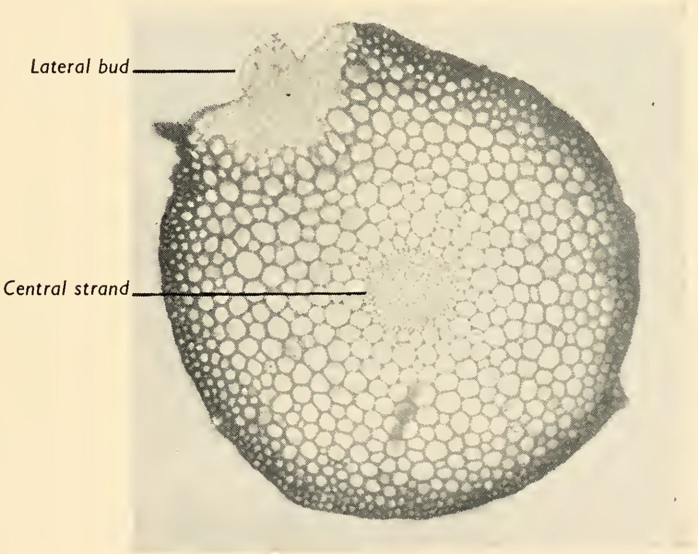

FIG. 400.—*Mnium hornum.* Transverse section through stem of the gametophyte, showing axial strand of hydroids and thickened outer cortex. Note the absence of any supply of conducting tissue to the lateral bud.

plants this inner layer of the cortex is showing some specialization. The cells of the cortex become progressively smaller and thicker-walled towards the exterior, and on the outside there are one or two layers of very small strongly thickened cells which function as an **epidermis.**

On the lower part of the stem arise long, brown-walled, repeatedly branched filaments of cells termed **rhizoids.** The cell partitions in these rhizoids are oblique, and close to these partitions branches arise, which may branch again and again in the same way. It is interesting to note that there is a considerable similarity between the structure of these rhizoids and the protonema, which we shall consider later. This close similarity is further exhibited by the fact that rhizoids if kept damp and exposed to light are capable of producing protonemal branches from which fresh plants can arise.

Here and there in the cortex small isolated groups of thin-walled cells occur, which in coloration and general structure resemble the elements of the central cylinder. We may regard this central cylinder as a very primitive type of conducting system, by means of which material in a liquid form can be transferred from one part of the plant to another, and these isolated bundles of cells lying in the cortex may be regarded as very simple foliar bundles or leaf traces. They are continuous with the midribs of the leaves, but they do not connect with the central cylinder and end blindly in the cortex. Although in *Mnium* these foliar bundles do not join the central cylinder, we shall find in the more specialized type, *Polytrichum*, that such continuity exists.

The apex of the stem possesses a single large **apical cell,** which is shaped like a three-sided pyramid with the base uppermost. This cell cuts off daughter cells from each of its three sides in turn, the nucleus rotating, so that the plane of nuclear division is parallel to each side successively. Each daughter cell, by division, builds up a segment of new stem tissue, and from each such segment a leaf develops. The leaves thus form a close spiral succession, each leaf being separated from its neighbours in the spiral by one-third of the stem's circumference. This arrangement is described as a **one-third phyllotaxy** (see Chapter XXII).

Lateral buds are developed from the base of the apical segment which forms a leaf, though not from all of them. Torsion of the stem during growth carries these buds sideways so that they are never directly under the leaf formed on the same segment, but usually appear as if axillary to one of the lower leaves. These buds may either remain dormant or may develop into side branches.

The leaf is narrow and pointed, measuring about 1 mm. by 5 mm. It consists of a central **midrib** which terminates a little below the point, and a single-layered **lamina** on either side of it (Fig. 401). The cells of the midrib are very elongated and thick-walled. The cells of the lamina are parenchymatous, whilst those along the edge of the leaf are like those of the midrib, elongated and strongly thickened. These outer cells bear, at approximately equal distances, pairs of sharply tapering **teeth,** formed of one or two cells, and similar teeth are also scattered along the back of the midrib. In section the midrib is seen to project more on the under than on the upper surface of the leaf, and in it towards the lower side there are a number of thin-walled cells continuous with the conducting cells of the foliar strands in the cortex (Fig. 402).

Fig. 401.—*Mnium hornum.* Leaf showing midrib and paired teeth on thickened margin.

Although *Mnium* is provided with abundant rhizoids and with a central strand of elongated cells in the stem, it has been shown by experiment that a considerable amount of water is carried up by capillarity on the surface of the plant and absorbed directly by the thin-walled cells at the apex and at the leaf bases. In many Mosses the amount so absorbed greatly exceeds the amount carried up internally. *Mnium* is an exception in this respect in that more water ascends through the axial cylinder than by the surface, and this may be due to the fact that its leaves are more widely spaced than is the general rule.

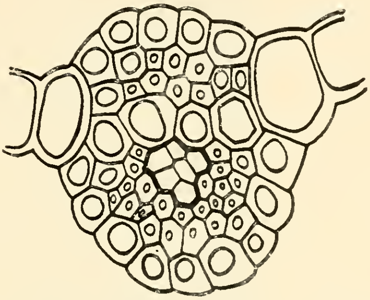

Fig. 402.—*Mnium hornum.* Transverse section of midrib of leaf showing strand of thin-walled hydroids surrounded by thickened fibre cells. (*After Muller-Berol.*)

Sexual Reproduction

As we have already said, the sex organs are borne on different plants, enclosed in a rosette of leaves termed the **involucre.** The head of the sex organs is sometimes called a **gametoecium,** and the leafy shoot the **gametophore.** Towards the centre of the gametoecium the leaves become progressively smaller, and in their axils, and particularly the axils of the inner ones, the sex organs develop, together with special filamentous structures termed **paraphyses.** Beneath these reproductive heads the stem broadens out, forming a flat **receptacle,** and in this region the central conducting tissue also broadens out and ends in a disc.

THE ANTHERIDIUM

The **antheridia** are spindle-shaped bodies, somewhat rounded at both ends, and supported on short stalks. A single receptacle bears from twenty to fifty (Fig. 403). The antheridium arises from a superficial cell of the receptacle which divides into two, the lower cell forming the stalk, and the upper the antheridium. The upper cell then divides so as to produce an apical cell, and from it about seven segments are cut off on each side. Walls are then laid down parallel to the surface of the antheridium in such a way that a single-layered wall is formed around it. From the central cells the **antherozoids** are developed, and when mature they escape through an opening at the apex of the antheridium (Fig. 404).

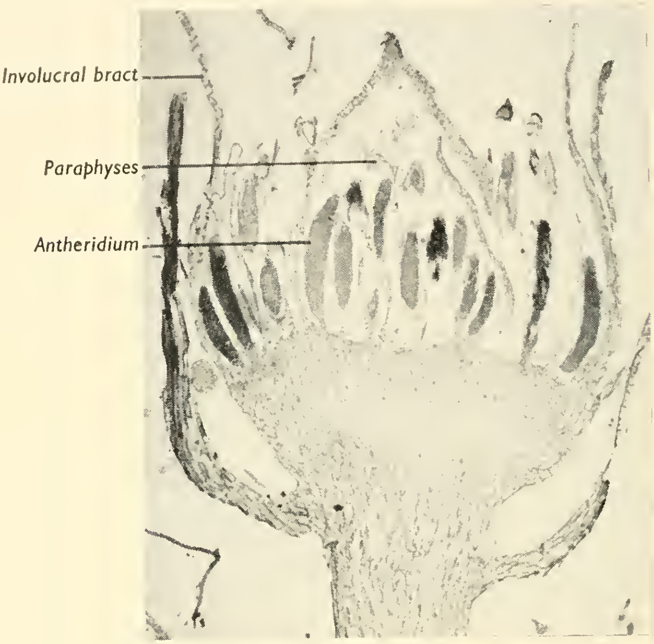

FIG. 403.—*Mnium hornum.* Vertical section through antheridial head showing broadened apex of stem and elongated antheridia surrounded by involucral bracts.

THE ARCHEGONIUM

The plants bearing the archegonia are generally considerably shorter than those bearing the antheridia and are somewhat darker in colour. The leaves at the apex close over the archegonia, protecting them during their development (Fig. 405). The **archegonia** are borne in the axils of leaves in the same way as the antheridia, but fewer archegonia are usually produced. The development of the archegonium is initially similar to that of the antheridium.

From a superficial cell on the top of the receptacle a stalk cell is cut off below, whilst the upper cell divides by three oblique walls, producing a tetrahedral cell, with its apex projecting downwards and its spherical base

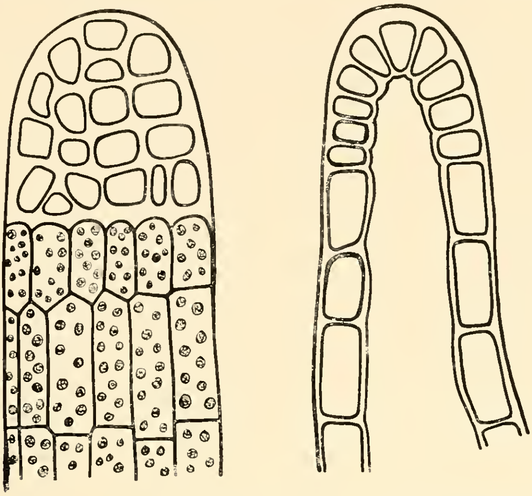

FIG. 404.—*Mnium hornum.* Apex of antheridium showing the operculum by which the antheridium opens. (*After Lorch.*)

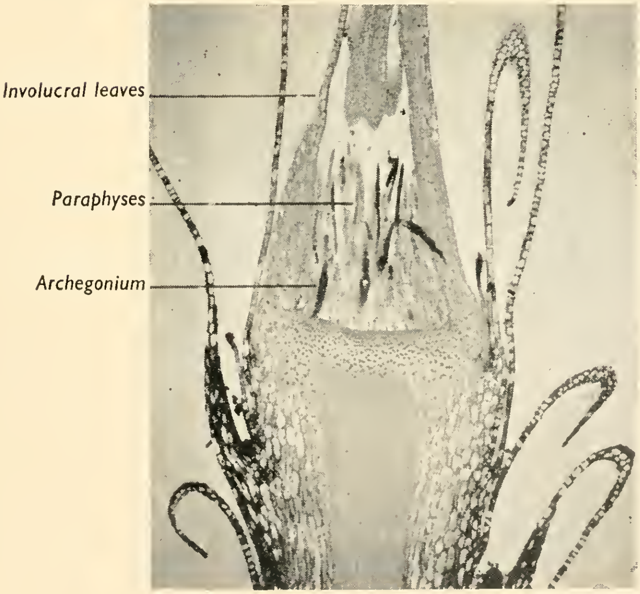

FIG. 405.—*Mnium hornum.* Vertical section through archegonial head showing archegonia, paraphyses and involucral bracts. Note that the axial conducting strand in the stem terminates just below the gametoecium.

upwards. This cell then divides by a transverse wall cutting off a central cell and an upper cap cell. From the peripheral cells the wall of the archegonium is formed, whilst the central cell gives rise to the **oosphere** and the cells of the **neck canal.** It will be seen, then, that the development of the archegonium in *Mnium* is essentially similar to that in *Pellia*. Scattered among the archegonia are numerous paraphyses similar to those found in the male plants. These paraphyses are composed of a single row of cells which gradually enlarge towards their apex. Their walls are often brown in colour, especially in the lower part, but all the cells contain chloroplasts.

Fertilization is effected in the same way as in the Liverworts. It usually occurs in May. The antherozoids migrate from the antheridia of the male plant to the top of the neck of the archegonium and make their way down, but one only fuses with the oosphere. We have already discussed in our consideration of *Marchantia* the means by which the antherozoids are enabled to make this journey. In *Mnium* it is even more difficult to see how the extremely delicate antherozoid contrives to make its way from the male plant to the female. Nevertheless from the number of capsules which are produced on any clump of Moss we conclude that no insuperable difficulty is encountered. Presumably fertilization can only take place when the Moss plants are well covered with moisture, to which the paraphyses contribute by water secretion, but it is worth while to consider the relative simplicity of fertilization among the aquatic Thallophyta and the difficulty which must have been experienced by plants as soon as they migrated to the land.

Development of the Sporogonium

Though more than one archegonium may be fertilized, normally only one sporogonium develops on each shoot of the female Moss plant. Although fertilization occurs in May, the development of the sporogonium is not complete until April of the following year.

The oospore divides into two by a transverse wall, and each cell then divides further so as to produce a spindle-shaped structure of small-celled tissue, with a large cell at either end (Fig. 406). From one end of this tissue the **foot** develops, by means of which the embryo is anchored into the tissue at the base of the archegonium. The **seta** or stalk of the sporogonium develops from the lower middle cells of the embryo, whilst the capsule is formed from the whole of the upper cells. As growth continues the foot makes its way downwards through the receptacle of the gametophyte and comes into contact with the top of the axial strand of conducting tissue in its stem. Although no cellular fusion occurs between the two tissues it will be realized that in this position it is enabled to obtain the maximum amount of water and other materials passing up the conducting cells.

For some time the **seta** remains quite short, but when it increases in length the body of the archegonium also continues to grow, and for a time keeps pace with the development of the sporogonium and acts as a cover to it. The neck of the archegonium shrivels, but when eventually the body of the archegonium is ruptured, at its base, all the upper part is carried upwards, covering the capsule with a cap called the **calyptra.** This remains as a covering to the capsule for only a comparatively short while. It turns brown, and before it is finally thrown off it splits along one of its tapering sides.

The structure of the capsule is somewhat complicated (Fig. 407). The body is shaped like a barrel, with a cone at either end. The seta is thin, with highly thickened outer layers of cells and a central strand very like that of the gametophyte axis. At the base of the capsule the seta enlarges conewise into the **apophysis,** a mass of tissue containing chloroplasts, which is attached to the lower end of the barrel or **theca** and marked off from it by a slight furrow. The apophysis contains an axial strand of conducting cells continued upwards from the seta. It also possesses numerous **stomata** (Figs. 408 and 409), very much like those of the Angiosperms (see Chapter XXII), and a rudimentary palisade layer of chlorophyllous cells, by means of which it can carry on photosynthesis. In the centre of the theca is a column of large-celled tissue termed the **columella,** and around the columella lies a layer of **archesporium,** from the cells of which the **spores** are formed. Outside this is a cavity containing loosely attached cells, with chloroplasts, partly filamentous in form, which wither away when the capsule is ripe. The spores are liberated into the space thus left. The outer wall

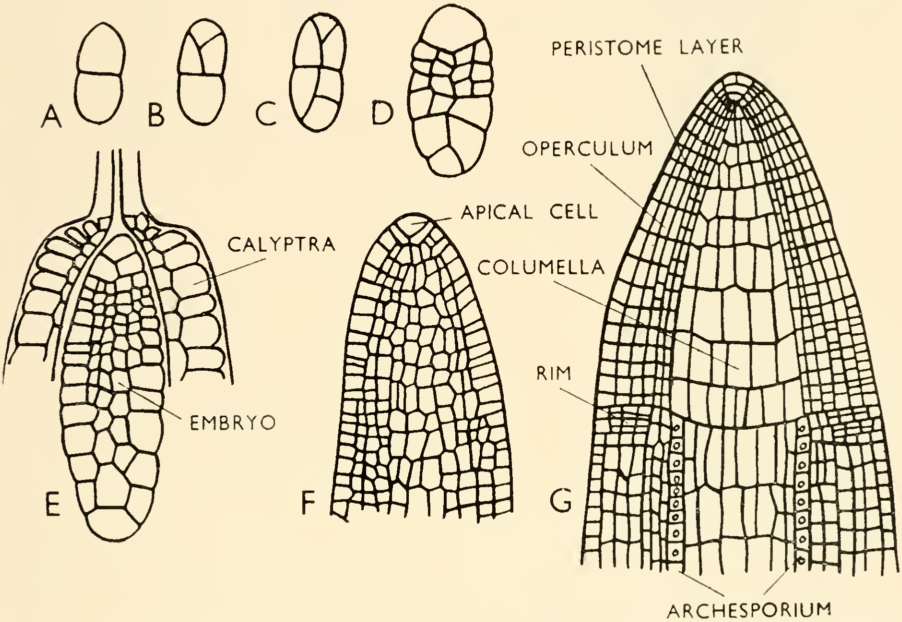

FIG. 406.—*Mnium hornum.* Development of sporogonium from oospore. A to D, Early stages in segmentation. E, Spindle-shaped embryo with apical cell at each end enclosed by calyptra formed from wall of archegonium. F, Upper half of embryo in more advanced stage showing differentiation of capsule wall and central tissue. G, Operculum and upper part of theca showing principal tissues differentiated. (*From various sources.*)

of the capsule is made up of several layers of cells, also with chloroplasts, and is covered by a well-defined epidermis, whose cells are more strongly thickened on their outer walls.

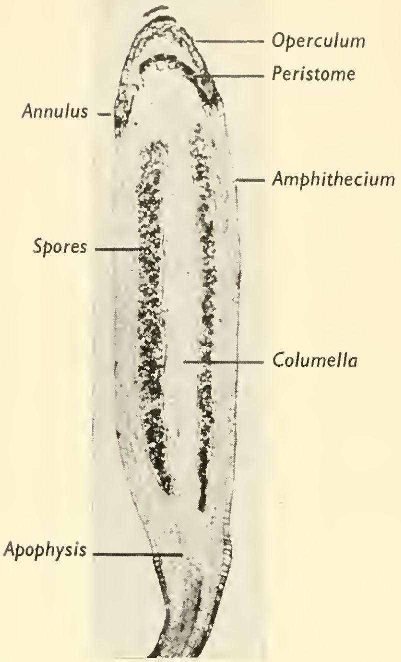

FIG. 407.—*Mnium hornum.* Median longitudinal section through mature sporogonium.

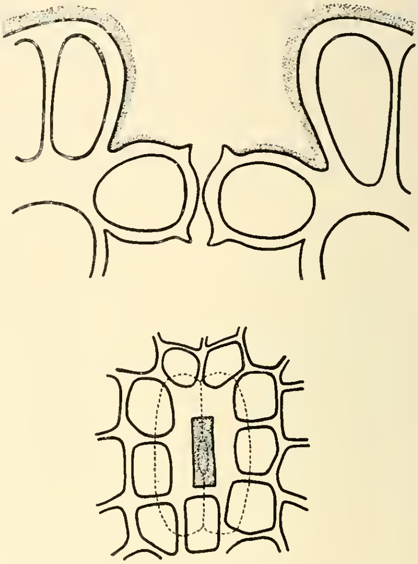

FIG. 408.—*Mnium cuspidatum.* Stoma on apophysis in cross section and in surface view. (*After Haberlandt.*)

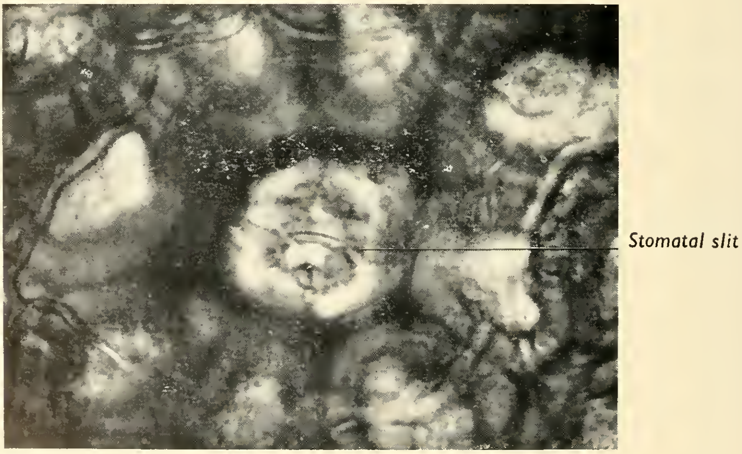

FIG. 409.—*Mnium hornum.* Stoma from external surface, showing slit.

The spore walls are brown and highly cuticularized, and often covered on the outside with tiny warts. The spores arise, as in the case of *Pellia*, from a spore mother cell, whose nucleus divides into four, during which reduction division takes place, so that before separation the four spores form a tetrad. Each is marked with a triradiate ridge caused by their close packing in the tetrads. As the spores develop, the tissue around the spore layer breaks down, and the loose tissue outside it withers away so that the spores are distributed over the whole of the space or **spore sac** between the columella and the wall of the capsule. At this stage the individual spores each contain chloroplasts and a considerable amount of reserve material in the form of oil. There is a very thin inner wall and a conspicuous cuticularized outer wall.

We must now consider the complex structures which constitute the cone of tissue, called the **operculum,** at the top of the capsule. In this tissue there arises a structure which is termed the **peristome.** The peristome consists of an inner and outer series of teeth, each series containing some sixteen teeth, composed of strips of specialized cell wall. These teeth are built up from a dome-shaped layer of cells whose outer and inner walls are cutinised. The radial walls are of unaltered cellulose (Fig. 410). When mature the cellulose walls and the cell contents disappear and the two cutinized walls alone are left, which split longitudinally into the outer and inner rings of teeth respectively (Fig. 411). These peristome teeth are **hygroscopic,** that is, they react to the influence of moisture. In damp weather the outer peristome teeth bend inwards, covering the inner peristome and effectively preventing the spores from escaping. In dry weather all the teeth bend outwards thus enabling spore discharge to take place (Fig. 412). The spores themselves are shaken out of the capsule by the action of the wind, for when mature the base of the capsule bends over so that the apical end is downwards, and the spores drop out readily when the peristome teeth open and allow them to do so. The mature seta is also hygroscopic, and its twisting movements assist in spore dispersal.

The peristome is covered during development by the surface layers of the operculum. This covering finally detaches itself from the peristome teeth and from the top of the theca and falls off, revealing the rings of teeth. Its dehiscence is assisted by the presence of a ring of large thin-walled cells, the **annulus,** at its base, the swelling of which causes its detachment from the **rim** of the theca, which is formed of several layers of very thick-walled cells, to which the peristome teeth are attached (Figs. 413 and 414).

The central tissue of the operculum, together with the top of the columella, wither away when the capsule is ripe, so that the dropping off of the lid leaves the capsule open at the top, except for the rings of teeth.

We see then that the top of the capsule has three protections. Firstly there is the calyptra, which is shed at an early stage, then there is the operculum, which remains until the peristome is mature, and finally, after this too has dropped off, there are the teeth of the peristome, which regulate the discharge of the spores according to the condition of the weather.

From a comparison of the capsule of the Moss with the corresponding structure in the Liverwort, we realize that the former is considerably more

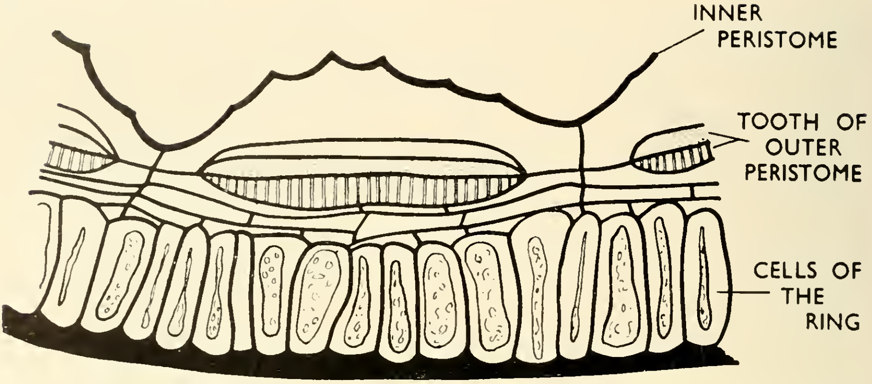

FIG. 410.—*Mnium hornum.* Section through the outer portion of the operculum showing the development of the peristome teeth from the opposite walls of the peristome cells. (*After Strasburger.*)

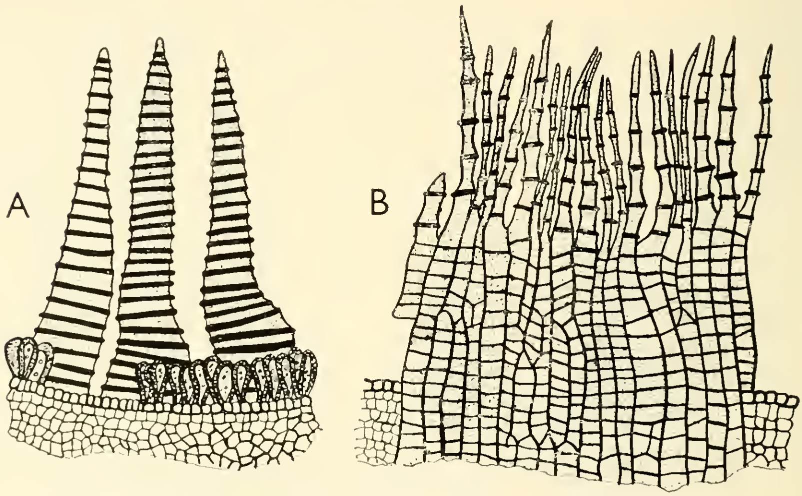

FIG. 411.—*Mnium hornum.* Peristome. A, Teeth of outer peristome. B, Teeth of inner peristome. (*After Strasburger.*)

complex and is more closely adapted to a land habitat. The peristome in particular, with its specialized mechanism for assuring that the spores shall only be discharged in dry weather, is a highly elaborate structure, but we shall find that analogous structures designed for regulating spore discharge occur in other groups of land plants.

Germination of the Spore

When the spore reaches the ground it remains dormant until conditions are favourable for germination, but in a damp environment the outer spore coat soon splits open, and the inner wall swells outwards and develops into the first cell. This cell elongates and divides, and from it is formed a series

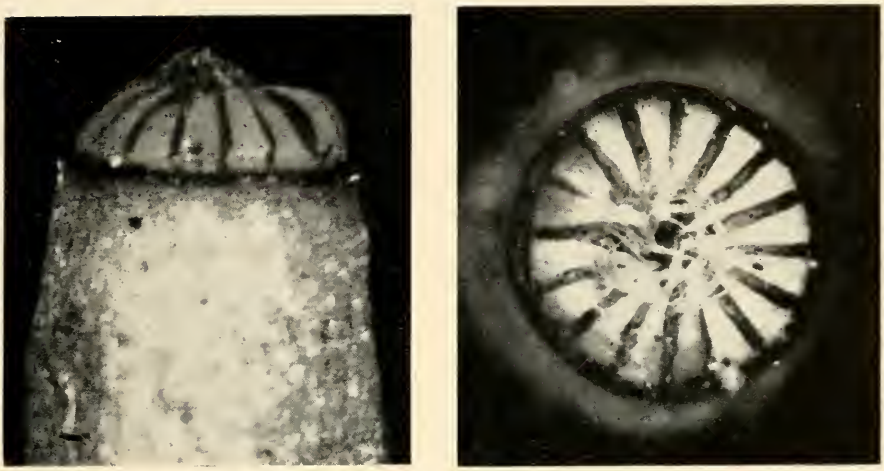

FIG. 412.—*Mnium hornum.* Apex of sporogonium after removal of operculum, showing peristome in side and top aspects.

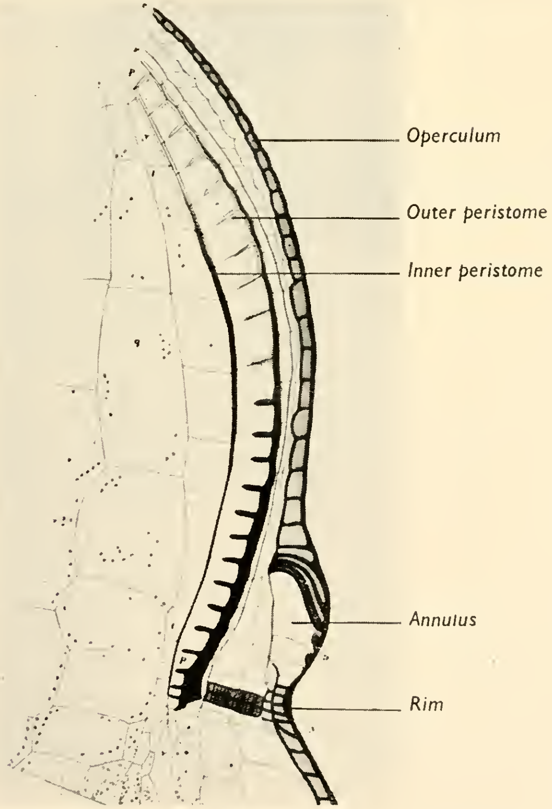

FIG. 413.—*Funaria hygrometrica.* Longitudinal section through part of the operculum and top of theca showing the relationship of the peristome teeth to the thickened rim. (*After Lantzius-Beninga.*)

of branched, multicellular filaments called the **protonema.** The branches of the protonema elongate very rapidly, growing by means of an apical cell, and in a short while produce a luxuriant, green, velvety growth. The protonema is characterized by its discoid chloroplasts and oblique transverse walls, which easily distinguish it from a Green Alga. From this protonema numerous small multicellular rhizoids are developed, and we find that in structure these rhizoids resemble closely those produced from the base of the leafy plant. They also have oblique cross walls. On short branches of the protonema tetrahedral apical cells develop (Fig. 415), and each of them forms the growing apex from which a young Moss plant develops. The protonemata are long-lived, and continue active long after the Moss plant has begun to develop. It is by their means that the large tufts or mats of Moss plants which we so often meet with are produced, and it is owing to

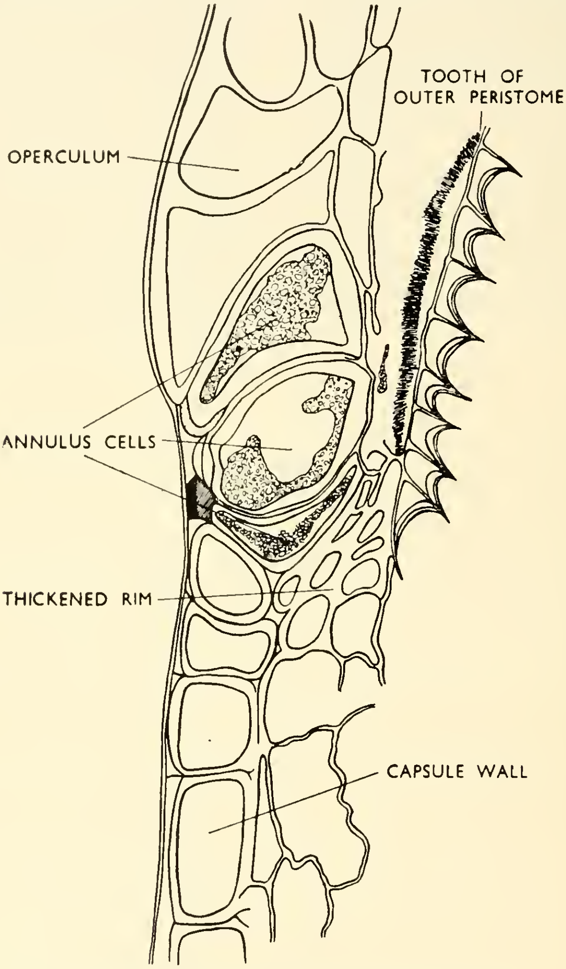

Fig. 414.—*Mnium hornum.* Vertical section through annulus and rim of theca. (*After Lorch.*)

them that separate Moss plants all grow so close together. As soon as the leafy shoot has been formed it develops its own rhizoids and severs its connection with the protonema which produced it. Since the protonema is the product of a single spore it follows that all the plants produced on it will be of the same sex, and it is only by the intermingling of two protonemata of different sex that male and female Moss plants can be produced side by side.

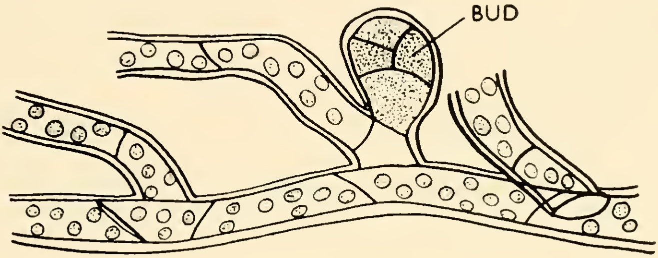

Fig. 415.—*Mnium hornum.* Origin of a leafy stem from a bud on a branch of the protonema. The apical cell is differentiated at the top of the bud. (*After Muller-Berol.*)

Alternation of Generations

The life history of *Mnium* shows the same alternation of generations as we found in *Pellia.* The Moss plant is a gametophyte, bearing either male or female reproductive organs. As a result of a fusion of gametes a zygote

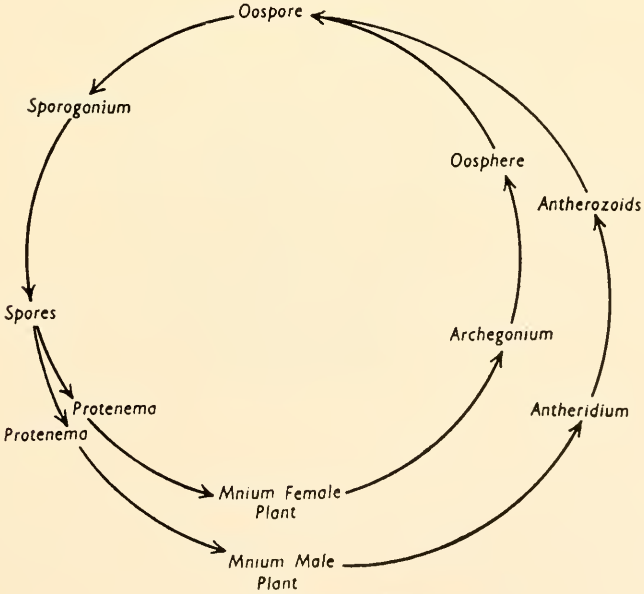

Fig. 416.—Life-cycle of *Mnium hornum.*

is produced within the archegonium, which develops into the spore-producing capsule, or sporogonium. This sporogonium, as we have seen, lives permanently upon the female gametophyte, and we may conclude from the fact that the foot is thrust down into the apex of the receptacle that the sporogonium obtains a considerable amount of food material from the gametophyte, and that it by no means relies entirely upon the chlorophyll cells which are developed in the capsule.

The living cells of the sporogonium have the power of producing secondary protonemal outgrowths, especially if they are in contact with damp soil. This protonema is, of course, diploid and the gametophytes which develop from it are likewise diploid. In such cases fertilization will produce tetraploid sporophytes. By the repetition of this procedure experimentally a 32-ploid plant has been arrived at, but this seems to be the limit, as the plant was sterile.

We can illustrate the life history of *Mnium* by Fig. 416.

Polytrichum commune

Our second example, *Polytrichum commune*, is one of the most highly developed types of Moss. It is found commonly in this country growing on moors and bogs and sometimes in woodlands, always preferring wet soils. In size it varies very considerably according to the environment, and sometimes when growing among long grass on a damp, peaty marsh, it may reach 30 cm. or more in length (Fig. 417).

FIG. 417.—*Polytrichum commune.* Plant with ripe sporogonia. Slightly reduced.

The anatomy both of the leaf and stem shows considerable complexity compared with the simple structures in *Mnium* (Fig. 418). The leaf is several cells thick. On the lower surface there is a well-marked epidermis composed of large cells whose outer walls are thickened; inside this are one or two layers of very small cells with very thick walls. The central tissue of the leaf is composed of thin-walled parenchymatous cells, among which are scattered small groups of tiny thick-walled cells. The upper surface is formed of a layer of large cells from which arise numerous longitudinal plates, five to eight cells high, which contain chloroplasts. The distal cells of each plate are enlarged in such a way that those of neighbouring plates almost touch one another. As a result, the chlorophyll-containing cells of the plates abut on to almost closed spaces. In some species the margins of the leaf flatten in a moist atmosphere and curl up in a dry one, so that the access of air to the parenchyma is controlled by a mechanism physiologically similar to that of the rolled leaves of higher plants.

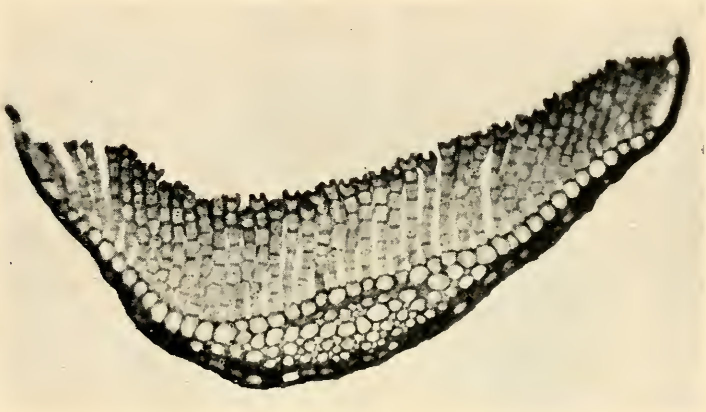

FIG. 418.—*Polytrichum commune.* Transverse section of leaf showing conducting cells in lamina and chlorophyll-bearing lamellae on upper surface.

These leaf plates are apparently a photosynthetic arrangement increasing the effective area of chlorophyll tissue, analogous to the chamber-filaments in *Marchantia.*

The stem shows distinct differentiation into a cortex and a central conducting tissue (Fig. 419). This central core consists of two obviously different tissues. Firstly a central strand of large, highly thickened cells which play an important part in water conduction, and are known as the **hadrome,** while, secondly, round this is a zone of small, thin-walled cells, called the **leptome,** supposed to have a food-conducting function. Around the conducting tissues there is a **mantle** of thickened cells containing starch grains, outside which we come to the extensive and thick-walled **cortex.** Finally there is an external **epidermis** of cells so highly thickened as almost to obliterate the cell cavities. Branches from the central tissue are given off to the leaves and are termed **leaf traces.** They can be seen traversing the cortex, each one being continuous with the thin-walled tissue in the leaf blade.

Below the leafy region of the *Polytrichum* stem the anatomy changes and we enter the portion known as the **rhizome.** The outline of the stem is here broadly triangular and the cortex is divided by three **radial strands,** which penetrate into the central cylinder, giving it a three-lobed outline.

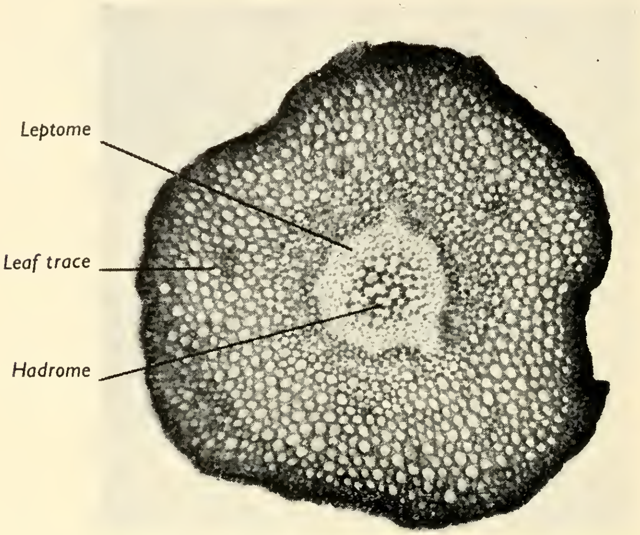

Fig. 419.—*Polytrichum commune.* Transverse section of aerial stem showing central conducting strand and leaf traces in cortex.

The outer tissues consist of three to four layers of **cortex,** the outermost layer of which is strongly suberized. The innermost layer consists of very large cells with thin suberized walls, known as the **endodermis.** Within this is the **central cylinder,** surrounded by a layer of thin-walled cells which represent a primitive **pericycle.** The greater part of the central cylinder is made up of thick-walled, somewhat elongated cells, forming the **sterome,** among which are scattered groups of empty, elongated cells, the **hydroids.**

The three radial strands start from groups of thick-walled cortical cells, while their inward ends, embedded in the central cylinder, consist of thin-walled **leptoids,** corresponding to the leptome in the upper stem. This inner group of leptoids is separated from the tissue of the central cylinder by a single layer of small cells containing starch, called the **amylome.** The triradiate structure of the central cylinder, with three separate leptome strands, affords a striking analogy to the alternating arrangement of vascular tissue in the root structure of higher plants, which bears the same relation to the concentric arrangement of the stem, that the rhizome of *Polytrichum* does to the concentric arrangement of tissues in its upper stem.

In *Polytrichum* all these structures are extremely primitive (Fig. 420) compared with the conducting systems of the higher vascular plants. We must bear in mind that they are analogous, but not homologous, with those systems. By the term **homologous** we mean that a certain structure is of the same botanical nature as another similar structure or has been evolved from a common ancestral structure. Since the Moss plant is a gametophyte, and the higher plant with which we are comparing it is a sporophyte, it is obvious that these systems cannot be of identical nature.

SEXUAL REPRODUCTION

The **antheridia** and **archegonia** arise at the top of the leafy stems within an involucre of leaves as in *Mnium*, though here the leaves resemble the vegetative leaves, except that those of the male are reddish in colour. In the male plant, however, the apex of the stem terminates in a vegetative bud in the middle of the antheridial head, which, after the development of the antheridia, may grow out in the following year and produce a fresh shoot, at the apex of which more antheridia may be produced. This proliferation through the antheridial head may be repeated several times.

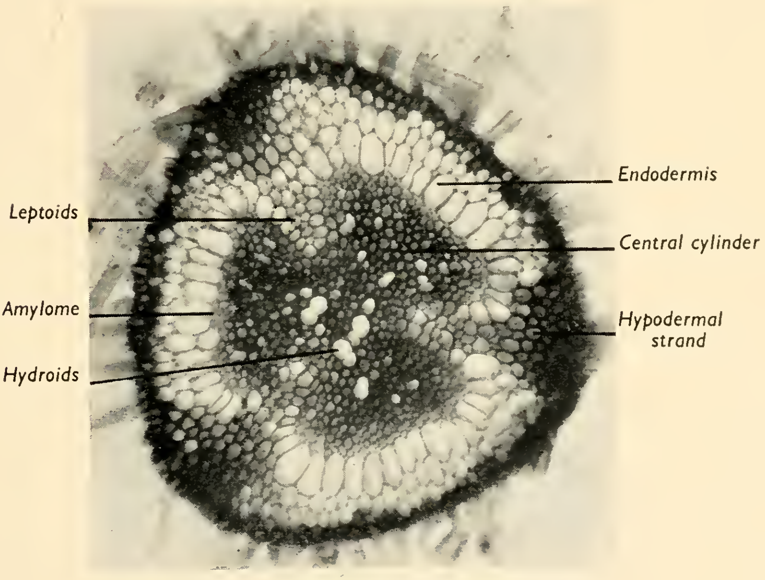

FIG. 420.—*Polytrichum commune*. Transverse section of rhizome bearing rhizoids.

The involucral leaves in the male head are not confined to the margin as they are in *Mnium*, but are arranged spirally from the vegetative apex outwards. The antheridia are produced in groups in the axils of these leaves so that the whole head is really compound and contains a variable number of these closely set antheridial groups.

Since the development of the antheridia and archegonia in *Polytrichum* is essentially similar to that in *Mnium* it will not be necessary for us to consider the stages in detail (Figs. 421 and 422).

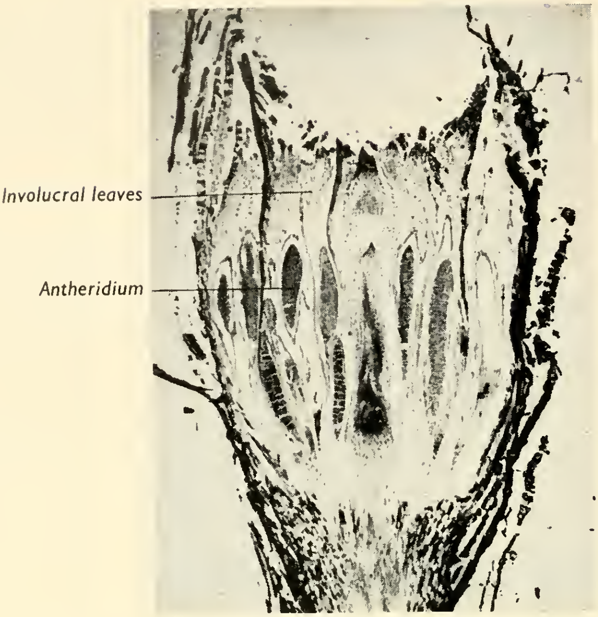

FIG. 421.—*Polytrichum commune.* Vertical section of male head bearing antheridia.

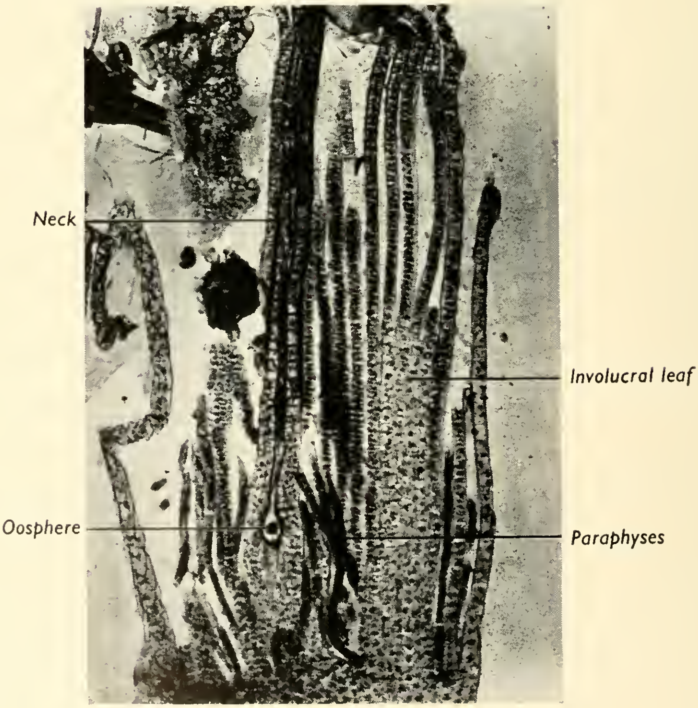

FIG. 422.—*Polytrichum commune.* Vertical section of female head showing a mature archegonium.

THE SPOROGONIUM

The **sporogonium** consists of a **foot, seta** and **capsule** which are developed in the early stages in the same way as those of *Mnium*, but the foot is prolonged further down into the gametophore and appears to be in more close contact with its tissues. The capsule is more highly specialized than that of *Mnium*, and shows certain additional features (Fig. 423). The seta and apophysis correspond in essentials to those of *Mnium*, though they are considerably larger. The stomata on the apophysis have, however, no pore opening and appear to be functionless. The seta may reach a length of several inches. The capsule, moreover, is square in section instead of being round.

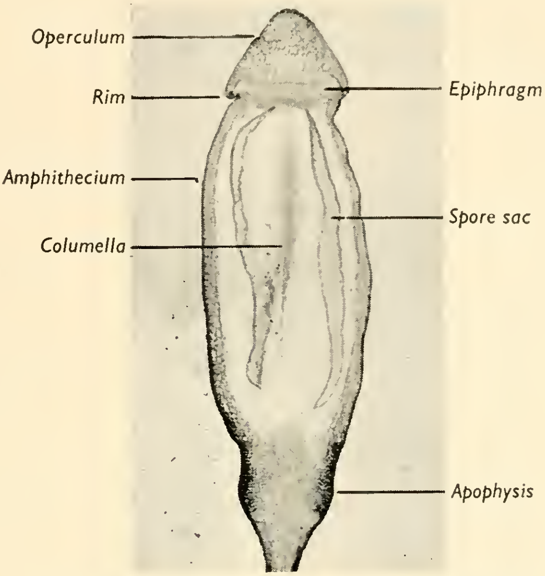

FIG. 423.—*Polytrichum commune.* Median longitudinal section of mature sporogonium.

In the mature **capsule** the sporogenous tissue forms a tube around the columella and is separated from it by air spaces which are traversed by filaments of assimilatory cells. A similar tissue is also developed between the spore mass and the wall of the capsule. This additional assimilatory tissue, or **aerenchyma,** as it is sometimes called, enables the capsule to obtain more carbohydrate material from the air by photosynthesis, and it will be noticed that since this tissue surrounds the spores they are in a very advantageous position to receive the maximum amount of food material.

The apex of the capsule also shows certain differences from that of *Mnium* (Fig. 424). The calyptra, which is carried up by the elongating seta, remains attached to the top of the capsule for a considerable time. It develops a brown colour, and grows after its separation from the basal part of the archegonium, forming a shaggy, hairy cap which covers the whole capsule, whence the name " hair moss " is sometimes given to species of *Polytrichum.* The operculum is conical, with a long beak or **rostrum,** and there is no well-marked annulus, though the theca has the usual thickened rim. The peristome teeth are short and stout, formed of groups of sclerotic cells, not of mere strips of cuticle as in *Mnium* (Fig. 425). They do not move hygroscopically but form a ring of rigid teeth when the operculum has fallen off. The top of the columella is expanded into a flat disc, the **epiphragm**, which fills the space inside the ring of peristome teeth and is attached to their tips (Fig. 426). The openings between the teeth thus form a ring of pores like those round the top of a poppy capsule, and the spores are dispersed through these pores by the force of the wind shaking the sporogonium. The pores are left open by the drying and subsequent shrinkage of the interior columella tissue.

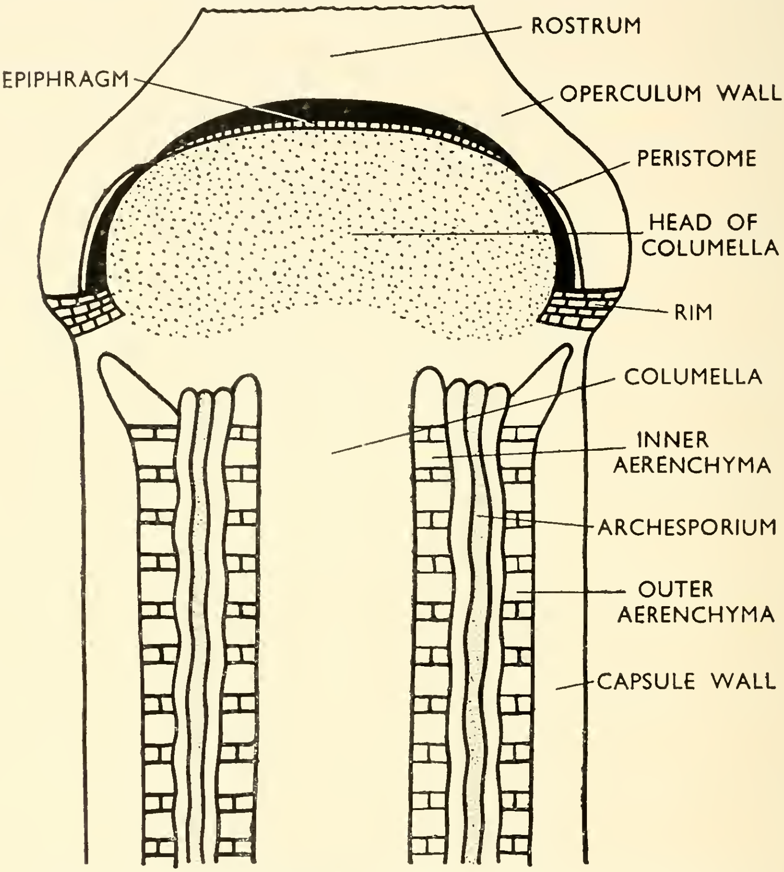

FIG. 424.—*Polytrichum commune.* Diagram of structure of operculum and upper part of theca. (*After Lorch.*)

The spores on liberation germinate to produce a **protonema,** which is similar in appearance to that of *Mnium*, and the new Moss plants arise as vegetative buds from its branches in the usual way. The older filaments of the protonema in *Polytrichum* sometimes become twisted together into cable-like strands, as in the mycelia of some Fungi (Fig. 427).

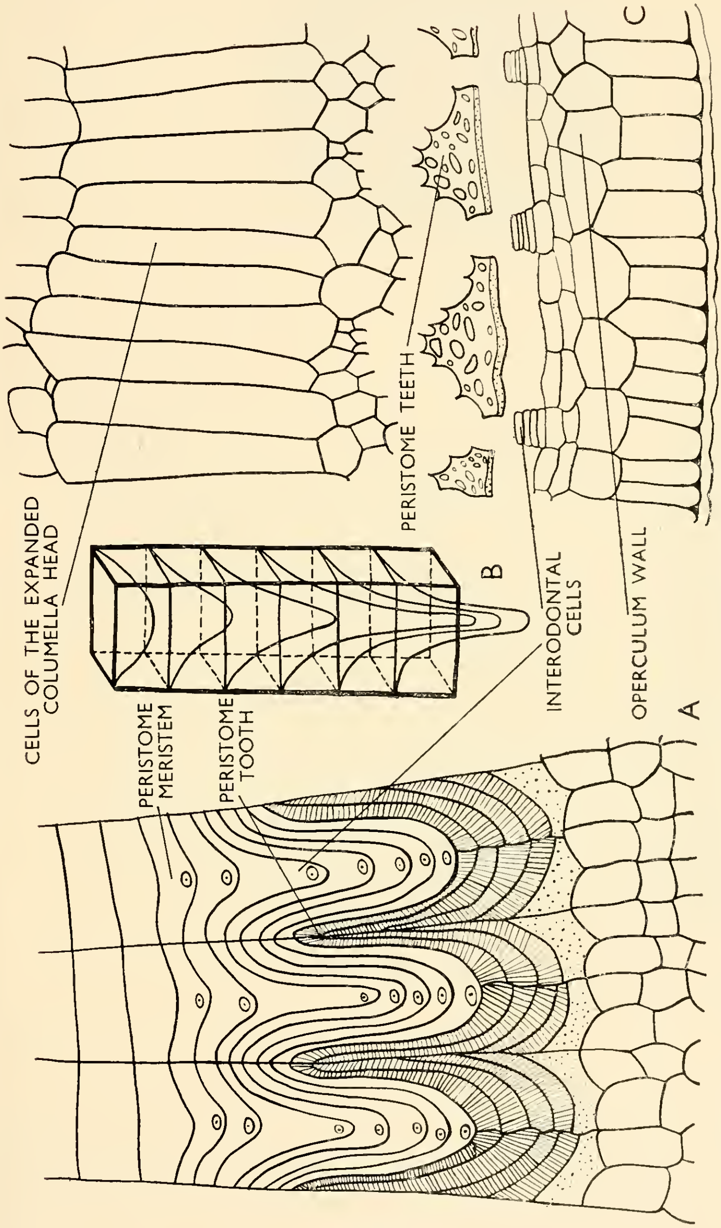

Fig. 425.—A, Tangential section of the operculum, showing the development of the peristome teeth from a zone of meristem which lies above them (diagrammatic). B, Diagram illustrating the way in which the horizontal walls of the meristem cells become invaginated downwards in the development of the peristome. The invaginations lie between the teeth, as shown in A, the lateral halves of each cell contributing to build up two adjacent teeth. C, Transverse section near the base of the operculum at the time of its separation from the capsule. (*A and C after Lorch, B after John.*)

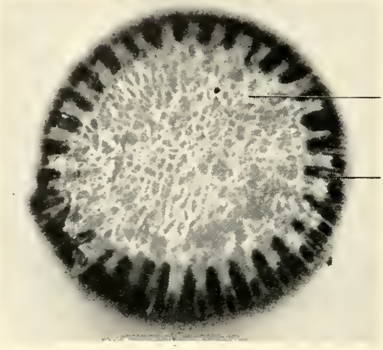

FIG. 426.—*Polytrichum commune.* Apical view of sporogonium after removal of the operculum.

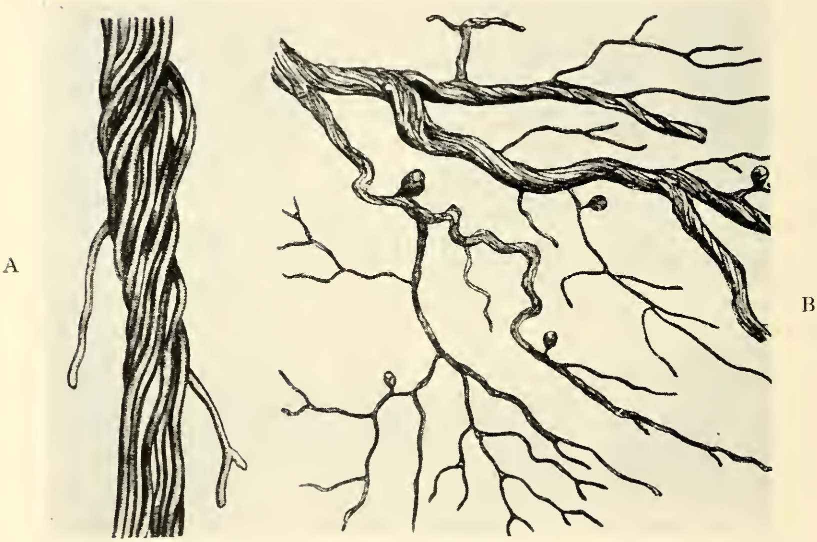

FIG. 427.—*Polytrichum commune.* Protonema. A, Cable-like strands of filaments in an old protonema. B, Buds destined to form leafy branches forming on a protonema. (*After Schimper.*)

Sphagnales

The order Sphagnales is monotypic, that is to say, it contains only a single genus, *Sphagnum*, which has, however, hundreds of species. They are among the largest Mosses in point of size, as well as among the most widely distributed, occurring in all parts of the world except the Arctic regions. Unlike most other Bryophyta they are markedly social, growing in extensive masses on boggy and peaty soils, where they often form the greater part of the plant covering. They contribute so importantly to the building up of certain types of wet peat that the term " sphagnum bog " is a recognized descriptive term in Ecology. They may also grow as submerged aquatics in peaty pools.

Although undoubtedly Mosses, they stand so far apart from the others in structure that they have been classed as a distinct group by some writers. In their vegetative structure they are unique, but in the spore capsule they show certain points of resemblance to *Anthoceros*, which in most other respects seems to be remote from them. Lacking any knowledge of their geological history, we must leave the question of their nearest relationships in abeyance. At the present day the chief centre of distribution of the genus is in Brazil, and it probably only reached Europe in recent times, *i.e.*, about the beginning of the glacial period.

Sphagnum

It is unnecessary in this case to cite particular species types because they differ from one another on such small and often obscure points that a general description will serve for almost any species which may be examined (Fig. 428).

Fig. 428.—*Sphagnum sp.* Fertile plant with sporogonia. Slightly reduced.

Vegetative Structure

The germination of the spore produces a **protonema,** which is thalloid and lobed, not unlike a young plant of a Liverwort or a prothallus of *Equisetum* (Fig. 429). In poor light, however, the protonema may develop into filaments as in other Mosses, and the transformation into the thalloid form depends on the light intensity. Separated parts of the mature plant can either develop **secondary protonema,** though the power to do this is apparently restricted to the short apical shoots, or they may develop new leafy shoots directly from single cells, thus affording an excellent means of vegetative propagation (Fig. 430).

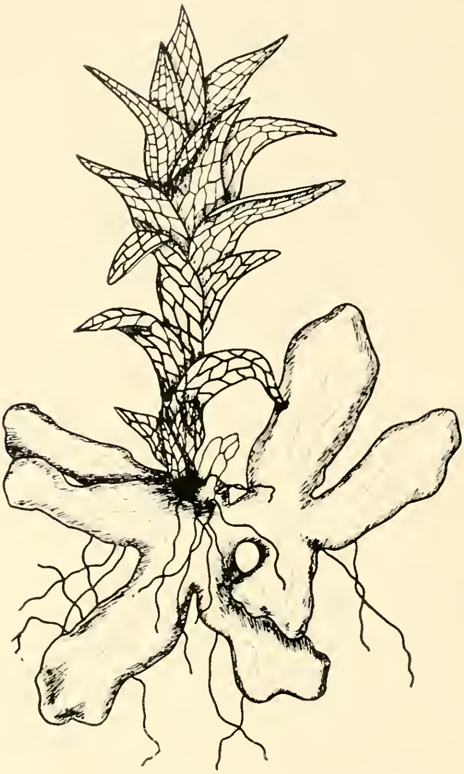

FIG. 429.—*Sphagnum sp.* Thalloid protonema giving rise to leafy shoot. (*After Velenovsky.*)

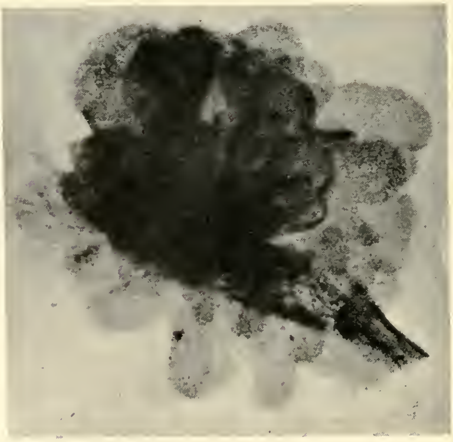

FIG. 430.—*Sphagnum sp.* Habit of protonema showing overlapping lobes.

The leafy gametophyte plant arises, as in other Mosses, by the formation of a three-sided apical cell from one protonemal cell, which by its rapid divisions builds up the leaf-bearing axis.

The mature plant of *Sphagnum* consists of an upright axis which has practically indefinite powers of growth. When growing in deep water it may reach a length of several feet. On land, however, the lower parts decay, so that the living stems are seldom more than a few inches long. Branching is normally lateral, from the leaf axils, though it does not occur regularly, and it is by this means that dense cushions of closely packed shoots are eventually formed.

The anatomical structure of the axis is somewhat variable. Typically three zones of tissue are present (Fig. 431); in the centre a **medulla** consisting of somewhat elongated, colourless cells, with collenchymatous thickenings on the longitudinal walls. Outwards the medulla passes over into a cylinder of **hadrome,** that is to say, of very thick-walled prosenchyma, which apparently forms a supporting tissue. There is no conducting strand comparable with that in *Mnium*, although the cells of both the above tissues have simple connecting pits, especially in the transverse walls. The outer layer is a spongy **cortex** (sometimes called the **hyalodermis**) of dead, empty cells, which, like those of the velamen in orchids, have large open pores in their walls, where the wall substance has been resorbed, and a network of cuticularized supporting ribs on the cell wall. This tissue actively absorbs water by capillary action and takes the place of rhizoids, which are not produced by the mature plants. In many species the side branches, though not the main axis, have the cells of the outer layer which stand at the points of leaf insertion, enlarged and flask-shaped, with the open neck turned outwards. These specialized absorption cells are frequently the homes of

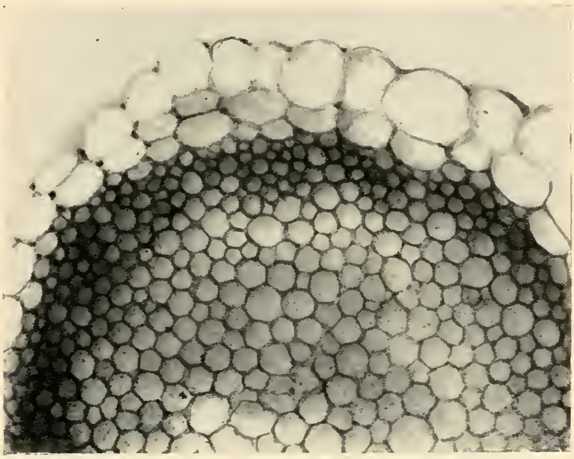

FIG. 431.—*Sphagnum sp.* Transverse section of leafy stem showing medulla surrounded by zone of thick-walled hadrome and thin-walled cortex.

Rotifers and other microscopic animals. They are the only perforated cells on the branches. Although there is no definitely lignified vascular tissue in *Sphagnum*, the plant contains 10 to 13 per cent. of lignin in its dry weight.

The power of water absorption by *Sphagnum* is remarkable and is an important factor in its Ecology. The dry moss can absorb up to twenty-five times its own weight of water. As it also transpires rapidly these reserves of water are a valuable safeguard as well as affording a means of getting the necessary nutriment from the very dilute solutions in which it lives.

The leaves are inserted very closely together on the side branches, but less so on the main stems. Their original arrangement is in three vertical rows, corresponding to the three sides of the apical cell, from which the segments are successively cut off. In the apical part of each stem this is clearly seen, but torsions soon alter this arrangement into a spiral with intervals of 144° between leaves. The base of each leaf springs from the hadrome cylinder and passes through the spongy cortex. This leaf base consists of cylindrical thick-walled cells, but the blade of the leaf, which has no midrib, consists of two kinds of cells, both of which are much elongated. The cells of one kind are wide and empty and resemble those of the cortex in having open pores and strengthening bands of cuticle. The other kind consists of very narrow living cells, with chloroplasts, which wind about between the others, making a fine, green network (Fig. 432). Species of *Sphagnum* are largely distinguished by minor variations of this structure, but in its main outlines it is characteristic of the whole genus and is a unique type of leaf (Fig. 433).

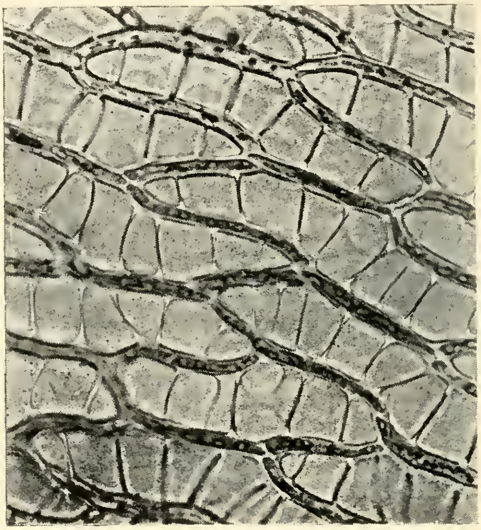

FIG. 432.—*Sphagnum sp.* Part of a leaf showing narrow chlorophyll-containing cells separated by large empty cells with cuticularized ribs.

The branches formed are of two kinds. Usually every fourth leaf on the main stem produces a side shoot in its axil, which branches into a tuft of three to six secondary branches, some of which stand upright, while others are longer and pendant, often clothing the stem thickly and acting as water conductors. Close to the apex the laterals are short and stout, forming a close, protective group around the apical bud. These subsequently lengthen and branch further, passing over into the condition of the mature laterals described above. Some of the upright branches may enlarge till they equal the main stem, and being separated from it by decay at the base, serve to multiply the plants vegetatively.

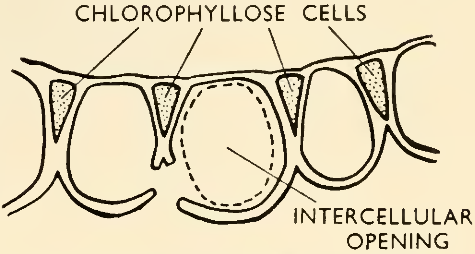

Fig. 433.—*Sphagnum cymbifolium*. Transverse section of leaf. (*After Warnstorf.*)

Sexual Reproduction

Sphagnum is sometimes monoecious and sometimes dioecious, that is, the sexes are sometimes on the same plant and sometimes on different plants. The male organs are borne singly in the axils of the leaves on special side branches, which are stouter than the vegetative shoots and often different in colour. Each antheridium is ovoid in shape and has a delicate stalk as long as itself (Fig. 434). It opens apically, and the valves thus formed turn backwards. It has been pointed out that the antheridia occupy the positions

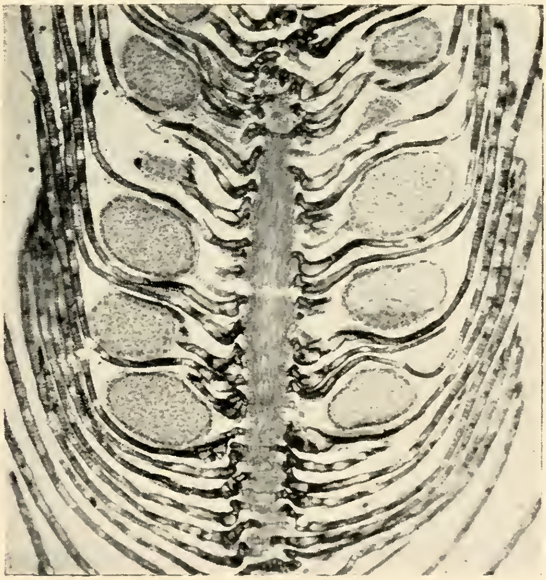

Fig. 434.—*Sphagnum sp.* Longitudinal section of an antheridial branch showing stalked antheridia axillary to leaves.

of axillary branches, whose initial cells have been transformed into antheridia at an early stage. The antherozoids closely resemble those of other Mosses.

The female branches are very short and clothed with leaves larger than the normal, diminishing towards the apex where there is a group of three archegonia of typical moss-form. The middle one grows from the apical cell of the branch, and the two lateral ones from the two last segments cut off from that apex before its transformation into an archegonium.

The Sporogonium

The ventral canal cell in the archegonium usually persists up till fertilization. Cases have been recorded in which it apparently replaces the true oosphere, and others in which it fuses with the oosphere, but nothing further is known about these anomalies. The normal zygote cell divides first transversely, and this is followed by other transverse divisions, so that the young sporophyte forms a filament of six to twelve cells before any longitudinal divisions occur. This is different from the development at this stage in other Mosses and recalls that in Jungermanniales like *Pellia*. Growth of the embryo is apical. The upper part of the filament becomes the spore **capsule,** the lower part forms the very short **seta** and the enlarged **foot,** which acts as an haustorium. The young sporophyte closely resembles that of *Anthoceros* in structure, but there is no basal meristem, and the capsule, instead of elongating, becomes spherical (Fig. 435). As in *Anthoceros* the archesporial layer develops from the amphithecium, the endothecium forming only the columella. The spore layer is dome-shaped, lying over the top of the rounded **columella,** and a disc-shaped **operculum** is differentiated, marked off by a **rim** of thickened cells. The outer layer of the capsule consists of cubical, strongly cuticularized cells, forming a very tough epidermis, but the inner tissues and the columella are thin-walled and delicate. There are abortive stomata present, which have no pores and whose guard cells contain no chloroplasts, though the latter occur in all the other cells of the capsule. The seta never elongates and the whole capsule remains, until mature, enveloped in a **calyptra** formed by the archegonial wall, the lower part of which forms a sac enclosing the foot, which is known as the **vaginula.** When the capsule is ripe the top of the gametophyte axis rapidly elongates, emerging from between the leaves of the archegonial branch and carrying up the whole sporophyte, with the foot still embedded in the vaginula, on a leafless stalk, the **pseudopodium.**

The thin-walled columella now shrivels away leaving an air space beneath the spore layer, and the outer walls shrink till the capsule becomes cylindrical (Fig. 436). This puts considerable pressure on the contained air, which cannot escape because there are no stomatal apertures. The thickened cells of the operculum, however, resist this shrinkage, with the result that a strain is set up at the rim. The air pressure eventually overcomes this, and an explosion occurs which blows off the lid to a distance of several feet and scatters the spores broadcast.

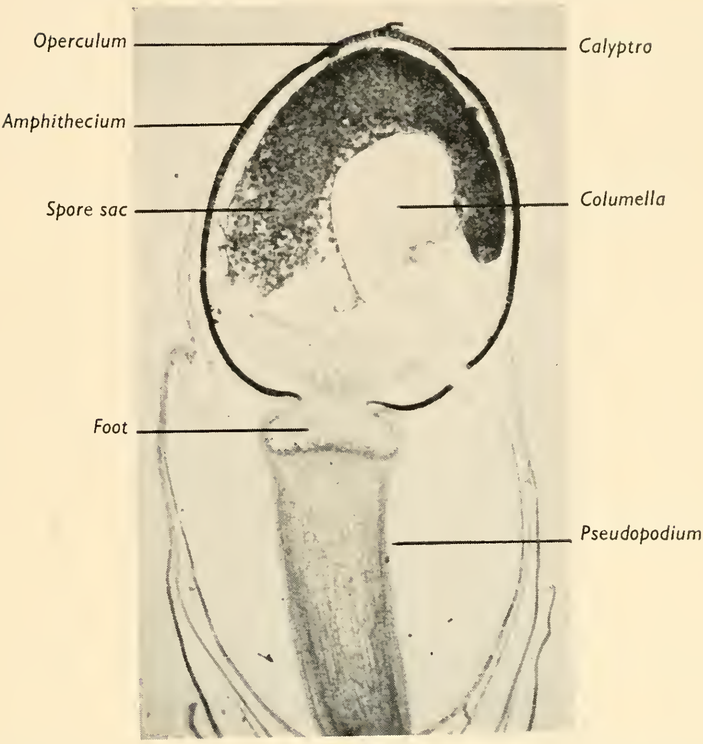

FIG. 435.—*Sphagnum sp.* Longitudinal section of mature sporogonium showing dome-shaped mass of spores and elongated pseudopodium.

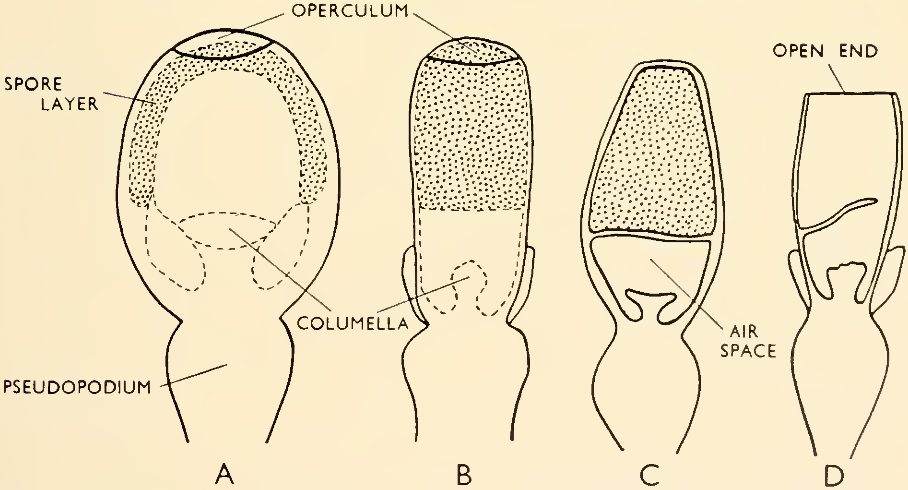

FIG. 436.—*Sphagnum.* A to D, Stages in dehiscence of sporogonium and discharge of spores. (*After Nawaschin.*)

For a plant which inhabits such wet localities *Sphagnum* is peculiar in having many features which only seem explicable as water-saving devices, such as the compact growth, the close overlapping and inrolling of the leaves, and the presence of specialized water absorbing and storing cells. In submerged plants, however, many of these features disappear, and it has been concluded that the normal bog-living plants suffer from occasional drought periods when these devices must operate to save the life of the plant. In Nature *Sphagnum* is highly calcifuge, *i.e.*, it grows only on lime-free soils and is very sensitive to the presence of Calcium salts in culture, though there is a good deal of difference between species in this respect. The plants give an acid reaction to litmus and contain quantities of insoluble organic acids of colloidal nature, like those of peat, which have the power of decomposing salts, even Sodium chloride, retaining the basic ions and liberating the salt-acids. This appears to be the plant's method of absorbing its mineral nutriment, and it is significant that those species living in water with the smallest amounts of dissolved mineral salts have the greatest content of acid. The effect of Calcium carbonate in solution is harmful only in the same way that other alkalies are harmful, namely, that it produces an alkaline environment which prevents the characteristic acid adsorption reaction and so kills the plant.

Origin of the Bryophyta

If we compare the life history of the Bryophyta with the algal examples of the Thallophyta which we have considered, we shall see certain obvious differences. The structure of the thallus, even in the simpler members like *Pellia*, shows a considerable advance above the Algae, for it is composed of a parenchymatous tissue derived from a single apical cell and not from the association of filaments, each of which grows more or less independently. We see, too, that there is some differentiation of the cells which compose the thallus. In *Pellia* this differentiation is slight, but as we pass to the more complex forms such as *Mnium* and *Polytrichum* we find this differentiation becoming more and more marked. Certain cells elongate and serve to conduct water, and in the most complex members we have seen that a system of conducting tissues may be formed, resembling that in higher plants, while branches of this conducting system pass out to the leaves, the main tract terminating, in the female plant, at the base of the developing capsule.

When we turn to consider the reproductive organs we find great changes in their morphology, and it is difficult at first sight to see any relation between the antheridium and the archegonium of the Bryophyta and the antheridium and the oogonium of the Algae. The most important change which has taken place has been the retention of the female gamete within the parent plant and its consequent loss of motility. It is true that in the Rhodophyceae the carpogonium is not liberated, and the oosphere is fertilized in the oogonial cell in *Vaucheria* and in *Saprolegnia*. But in none of these cases is there any cellular structure surrounding the oosphere comparable to the archegonium (Fig. 437).

One of the problems which has beset evolutionists has been to explain how the sex organs of the Bryophyta could have been evolved from those

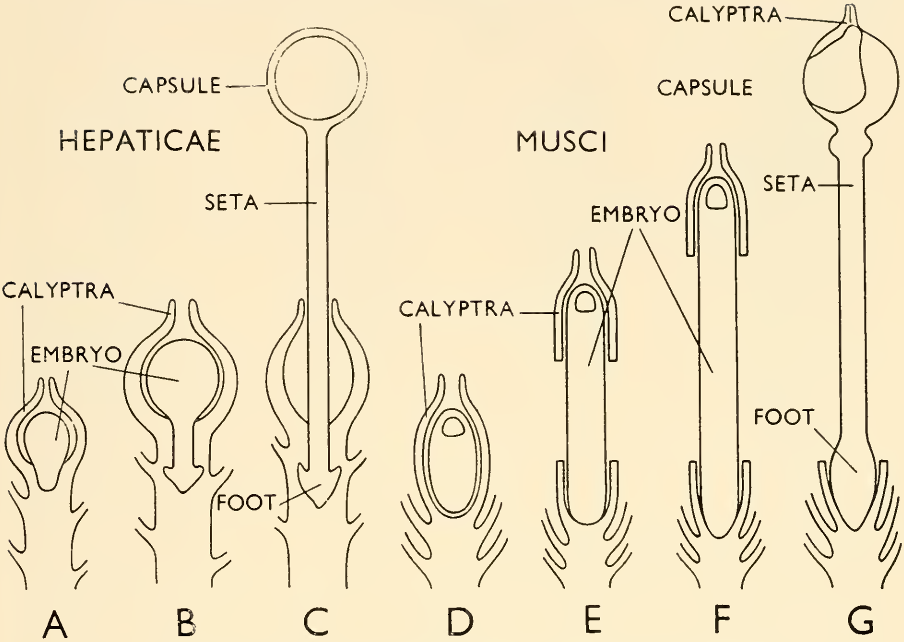

FIG. 437.—Comparison of the development of the sporogonium in the Hepaticae (A, B and C) and in the Musci (D, E, F and G). (*After Goebel.*)

of the Algae, and we will consider here one theory to account for their evolution. According to this view both the antheridium and the archegonium originated from gametangia of a type similar to those in *Ectocarpus* (Fig. 438). It will be remembered that in this plant we saw that the gametangium consisted of a number of cells, each of which gave rise to a gamete. It has been suggested that as a result of the migration on to land it was necessary to protect the gametes from desiccation, and as a result the outer layer of cells of the gametangium became sterile and functioned as a wall to protect the cells inside, which produced the gametes. It will be seen that by such a view it is comparatively easy to derive the antheridium. Here we have a structure in which the outer layer of cells constitutes the wall, whilst the cells of the interior divide up to form the antherozoids. The derivation of the archegonium is more complex, but it has been suggested that after the development of the superficial layer to form a wall, progressive sterilization of the interior cells occurred, starting at the apex and proceeding backwards. In this way it is explained that the neck canal cells were originally female gametes, which first of all lost their walls and then their cytoplasm, till in the typical archegonium they are represented by little more than nuclei. The ventral canal cell is a sister cell of the oosphere, and hence we may say that the ventral canal cell is a potential gamete, and in this connection it is interesting to note that there are cases on record in which both the oosphere and the ventral canal cell may be fertilized, and both of them commence to develop embryos, though there is no case on record in which the embryo

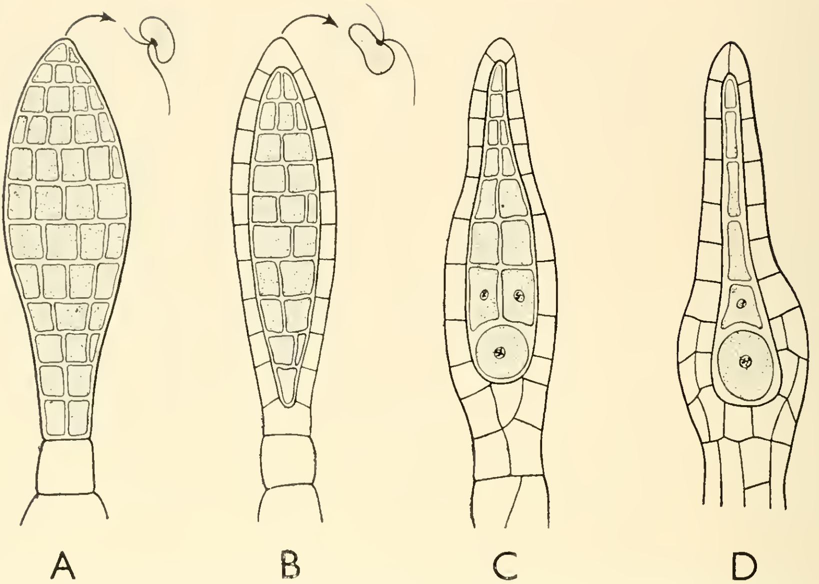

FIG. 438.—Diagram illustrating the possible evolution of the antheridium and the archegonium from a gametangium. A, Gametangium. B, Walled antheridium. C and D, Stages in evolution of an archegonium. (*After Davis.*)

derived from the fertilization of the ventral canal cell proceeds for more than a few cell divisions.

It must be clearly understood that in postulating this origin of the archegonium we are considering the matter from a purely theoretical aspect, we have no examples living at the present time showing stages in such an evolutionary series. In fact, gametangia of the multicellular type are only found in the Phaeophyceae, and it is not suggested that the Bryophyta originated from this group ; the question of pigmentation alone makes it very improbable.

In fact the evolutionary picture thus outlined is so vague and unfinished that one is driven to question the accepted idea of the derivation of the Bryophyta from the Algae. There is considerable evidence of reduction having taken place in some phases of the Bryophyte evolution, and it is not impossible that reduction, that is to say simplification, has been the keynote of evolution throughout the group. This idea, if accepted, would lead to the conclusion that the simplest members, which are those most aquatic in their habits, are really derived from more complex Bryophyta and have taken to an aquatic life secondarily.

Following out this scheme we would regard the highest Bryophyta, such as the larger Mosses, as being derived from a common stock with the Lycopodiales, and as having diverged from them by the development of the gametophyte rather than the sporophyte as the chief phase in the life history. This course did not prove as successful as the sporophyte line of evolution in the Pteridophyta, and the Bryophyta were gradually driven back more and more, upon moist, and finally upon aquatic habitats.

CHAPTER XIII

INTRODUCTION TO PLANT HISTOLOGY *

In the previous chapters we have been considering types of organisms in which the principal plant body is the gametophyte, but as we shall see in the next chapters the bodies of the Pteridophyta and Spermatophyta are sporophytes. These bodies are of great complexity, and before proceeding further it is necessary for us to consider in some detail the types of cells which contribute to their formation.

The study of plant tissues and the cells which compose them is termed **plant histology.** One important point must be made at the outset, namely that the study of plant histology is more concerned with the architecture of the cell in relation to the function which it performs than with its internal composition, and therefore it is the study of cell walls rather than the study of the whole cell. Moreover, as we shall see later, many of the types of cells which form tissues are really dead structures, containing no protoplasm, although they still serve important functions. For this reason the amount of material which is actually living and growing in a higher plant is a varying and uncertain quantity, depending on the proportion of living to non-living cells. This proportion is greatest in early life and it diminishes progressively with age. In the embryonic stage all the body cells are living and actively growing, but in the course of development the growth activity becomes very soon localized, particularly at the tips of shoots and roots, where the tissues retain the embryonic character throughout the whole life of the individual. Plants thus present an opposite condition to that in animals, in which growth is general in all organs until a specifically limited size is attained, after which it ceases. In plants, on the contrary, growth is localized from an early stage, but is maintained at these points more or less continuously. The size reached by a plant is therefore, in favourable circumstances, simply a function of its age.

Meristem

The embryonic tissue which forms the **growing regions** of the shoots and roots is called **meristem** (*meristos* = divisible), because these are the sites of rapid cell-multiplication. A certain proportion of the cells produced, subsequently enlarge, cease to divide, and acquire thickened walls or undergo other changes and are then added to the **permanent tissues** of the plant. This change from meristematic to permanent form is called **cell differentiation.** A certain number of residual cells, however, always retain

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* A more detailed treatment of the structure and development of tissues will be found in Chapters XX, XXI and XXII.

the meristematic character, so that meristem, in addition to forming permanent tissues, is also self-perpetuating. In most Pteridophyta the function of producing new cells is localized in a single **apical cell** instead of being distributed through a meristematic tissue. In this they resemble certain Thallophyta.

The tip of a stem is usually occupied by a bud, which is composed of immature leaves produced by the growing point itself. The latter lies in the centre of the bud, and a median longitudinal section will show that it is in fact the actual apex of the stem, which tapers rapidly within the bud, to end at this point. The meristem of the growing point is extremely soft, delicate and juicy, as seen with the naked eye. A similar tissue occupies the tip of the root, but no bud surrounds it in this case, because roots have no leaves.

Microscopically the cells of the growing point are small, fairly regular in size and shape and have thin, delicate cell walls formed of a mixture of cellulose and protein, with an intercellular layer of mucilaginous pectin. They have prominent spherical nuclei, which are very large relative to the size of the cells, and the cytoplasm is dense and completely fills the cells. When a meristem cell divides, each half quickly grows to the size of the original cell, thus doubling the amount of protoplasm. It follows that it is here that the chief synthesis of protoplasm goes on. The cells fit closely together, without intercellular spaces, and their shapes are those of plastic spheres in mutual compression, due to their active growth. They are either dodecahedra (twelve-sided) or tetrakaidecahedra (fourteen-sided). The youngest cells have no vacuoles and they never possess chloroplasts, though transitory starch grains may sometimes appear.

Opinion varies as to the exact limits of the term meristem. Some confine it entirely to the non-vacuolated cells, but there is a considerable interval between the first vacuolization of the cell and its completed differentiation, and many prefer to extend the term generally to all those cells which continue to divide, even when somewhat altered from their youngest form.

The meristem of the growing point is called the **apical meristem,** and the term **primary meristem** is applied both to it and to all meristem tissues derived directly from it. Thus the cambium in Dicotyledons and the meristems of lateral shoots are also usually primary meristems. In many Monocotyledons there are **intercalary meristems** at the bases of leaves, and similar embryonic regions occur in older parts of Dicotyledons. All these are primary meristems. True **secondary meristems,** *i.e.*, those formed from tissues previously differentiated, are rare, the chief example being the cork cambium (see Chapter XXI).

When we consider that the development of the meristem cells is responsible for determining the specific form of the plant and the structural anatomy of the older portions, it is obvious that it is the centre of many activities of great interest, about which we know very little. The evidence seems to show, however, that almost without exception the divisions of meristem cells are equational, and therefore that the potentialities of the cells produced are equal. There is little sign in plants of the primary segregation of germ cells and soma cells which Weismann suggested in animals. Theoretically every cell of the plant is **totipotential,** that is, it retains in itself the possibility of regenerating the whole plant, in suitable circumstances. Any actual limitations of this power are imposed by special conditions. The differentiation of cells is therefore explicable, not by inherent differences between them but by the influence of their environment, that is to say by differences of water and food supply, oxidation, etc., due to the position of the cell in the tissues.

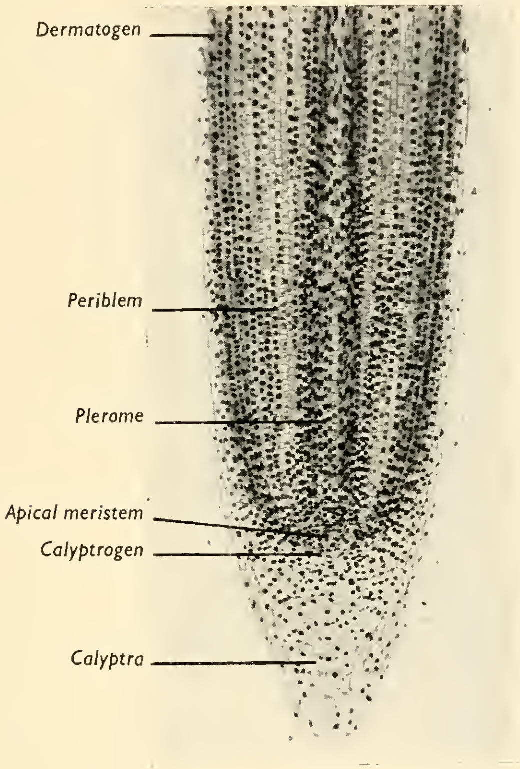

FIG. 439.—*Vicia faba.* Longitudinal section of root apex showing the histogens.

Even within the meristem some differentiation is apparent. In 1868 Hanstein named three zones, which he considered to be typical and which he called **histogens** or " tissue producers " (Fig. 439). The outermost was a single layer of cells named the **dermatogen,** which gave rise to the epidermis. Beneath this came an intermediate zone, the **periblem,** giving rise to the cortex and the inner tissues of the leaf. Centrally was the core or **plerome,** producing pith and vascular tissues. In cases where such layers can be seen these names still have a descriptive value and are frequently used, but the developmental significance assigned to them by their author is not consistent with fact. Frequently, indeed, the three zones cannot be distinguished, especially at the apex of the stem.

Modern studies have interpreted the meristem of stems as composed of two zones only (Fig. 440). These are the **tunica,** which consists of one or several peripheral layers of cells, enclosing the **corpus** or central core of tissue. The distinction between them reflects two different modes of growth. In the tunica, surface growth predominates and cell divisions are uniformly anticlinal, that is, perpendicular to the surface, with the result that the cells are regularly oblong in longitudinal section and each tunica layer remains distinct.* In the corpus, by contrast, volume growth is predominant and the planes of cell division and cell arrangement tend to be highly irregular. The maintenance of balance between surface and volume growth leads to constant adjustments which find their expression in the rhythmical alternation of minimal and maximal areas of the growing point, the latter being associated with the formation of external folds or leaf primordia (see also Chapter XXI). These zones are not " histogens " in Hanstein's sense but represent the distribution of growth patterns, which may vary considerably in different species.

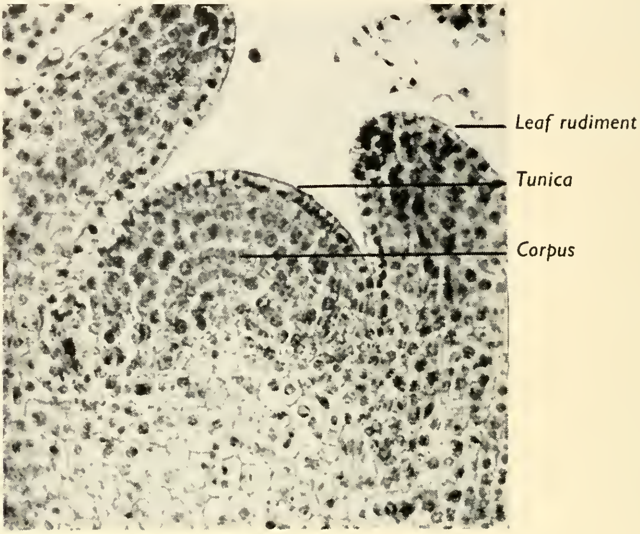

FIG. 440.—*Solanum crispum.* Longitudinal section of stem apex showing tunica and corpus.

Immediately below the corpus may often be seen a tissue which is called the **rib meristem,** distinguished by short, vertical rows of cells in process of vacuolization. These are formed from cells of the corpus which have repeatedly divided horizontally. As each row is produced from one original cell it has a common wall surrounding it. This tissue continues downwards into the pith.

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* As the tunica cells have no vacuoles their mutual pressure is only the lateral pressure due to growth. They therefore take the form of hexagonal prisms with their long axes anticlinal.

Elementary Tissues : Parenchymatous Types

Cells of the permanent tissues are loosely classified as either **parenchyma,** which are more or less isodiametric, or **prosenchyma,** which are elongated cells, usually of some specialized type ; they make up the conducting or **vascular tissues** and **fibres.**

The parenchyma cells are the least differentiated and collectively form the **ground tissue,** which is usually divided into the **medulla,** or **pith,** inside the vascular ring, and the **cortex,** outside it. The simple parenchyma cell (Fig. 441) is, in fact, the typical mature cell, as we have described it in Chapter II. The principal features of its differentiation from a meristem cell are :—

(*a*) Considerable increase in size, which is due to ;
(*b*) The multiplication and expansion of the vacuoles, which finally unite and occupy all the central part of the cell, thus limiting the protoplasm to a thin layer, or **utricle,** and pushing the nucleus to one side.
(*c*) The stiffening of the cell wall by the growth of a secondary cellulose layer inside the original wall.
(*d*) Rounding and contraction at the edges and corners of the cell, so that a system of narrow **intercellular spaces** appears, which contain air and play a part in the supply of oxygen to the tissues.
(*e*) In many cases the development of plastids, either leucoplasts in the deeper-seated cells or chloroplasts in those exposed to light.

As the parenchyma cell is a living cell, with a considerable internal hydrostatic pressure, its form is fundamentally spherical, that is to say, the figure of minimal area, and it is the physical necessity for assuming this figure, under the influence of internal pressure, which no doubt accounts for the separation of the cells at their edges as they become vacuolated. The sides of the cells are somewhat flattened by mutual pressure, giving the isolated cell the twelve-sided figure of a rhombic dodecahedron. This is the geometrical figure, with all its sides plane and similar, which has the least surface for its volume, and it is therefore the simplest form into which a given space can be completely partitioned. In section this figure is hexagonal, and therefore the cells of a perfectly uniform ground tissue will always appear approximately hexagonal in sections of plants organs. This outline is subject to deformation by the internal strains due to differing growth rates, but it can be very generally observed and should be kept in mind when making drawings of cellular structure.

The fascinating study of the physical principles of cell form and growth cannot be further pursued here, but will be found fully treated in " Growth and Form," by D'Arcy Thompson (Second Edition, 1942).

Parenchyma cells of irregular form are found occasionally, principally in the spongy tissue of the leaf, where neighbouring cells touch only at a few points, and there are large intercellular spaces. In some Monocotyledons

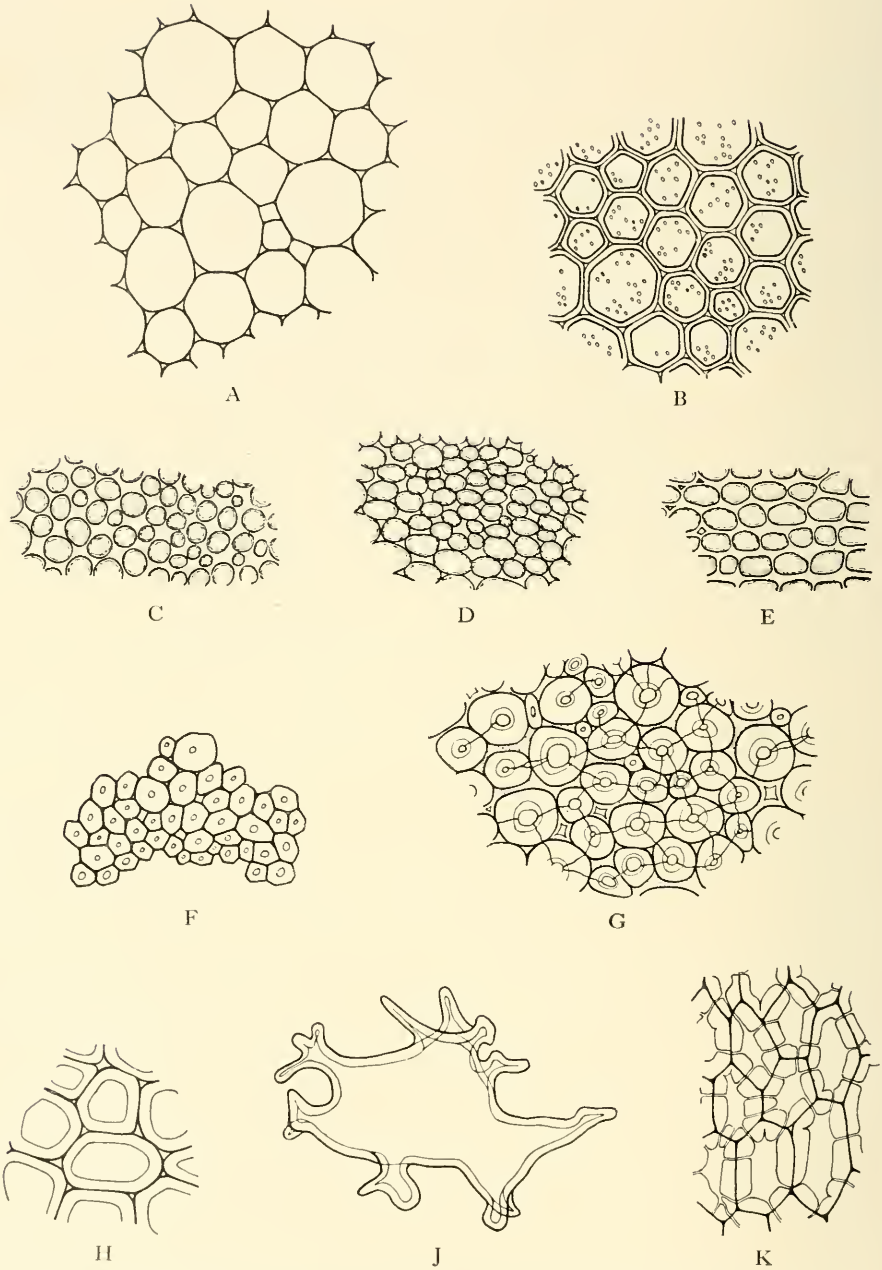

Fig. 441.—Types of cells. A, *Agropyrum repens*. Thin-walled parenchyma from stem cortex. B, *Cocculus sp.* Thick-walled parenchyma with numerous pits from stem pith. C, *Rumex crispus*. Collenchyma from stem cortex. D, *Beta vulgaris*. Collenchyma from stem cortex. E, *Aralia sieboldii*. Collenchyma from petiole. F, *Persoonia juniperina*. Sclerenchyma from leaf. G, *Pinus pinea*. Sclerenchyma from cone scale. H, *Magnolia grandiflora*. Stereids from root cortex. J, *Talauma hodgsoni*. Stereid from pericarp. K, *Podocarpus sp.* Stereids from testa.

also, notably in the pith of the Rush, *Juncus*, there are six-rayed, stellate, parenchyma cells attached only at the ends of the arms (Fig. 442). This appearance is due to local wall growth in the pith cells, which are held within a ring of resistant external tissues which have ceased to grow. As outward expansion is prevented the free portions of the cell walls fall inwards into catenoid curves.

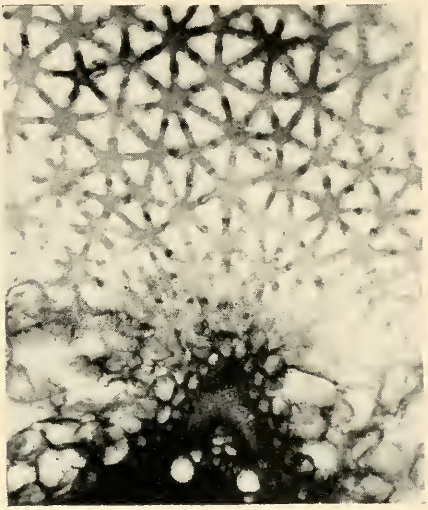

FIG. 442.—*Juncus effusus*. Transverse section of stem showing stellate parenchyma in pith.

Occasionally we meet parenchyma cells with thickened walls. The most important case is that of **collenchyma,** a tissue often found in the outer layers of stems and petioles, especially where ridges or angles exist. The cell walls are heavily thickened with cellulose, which may be regularly developed, but is usually irregular, forming especially in triangular masses, or trigones, where three cell walls meet. This seems to be a means of increasing mechanical strength.

Parenchyma cells may also become lignified, that is, the walls receive a deposit of lignin or hard woody matter (see p. 460). This often happens in old pith and in the parenchyma of the woody vascular tracts, or it may affect only small groups of cells embedded in soft tissues. The thickening of the wall is sometimes extreme, very little lumen being left unfilled. The lignin is laid down in concentric layers and is traversed by narrow, radial canals, often branched, which connect the wall to the central lumen, and are in fact pits, or more correctly pit-canals, leading to pits in the middle lamella. Cells of this kind are called **stereids,** or stone cells. They occur in many soft tissues, especially in fruits. A well-known example is in the flesh of the Pear. Stereids of extraordinarily irregular form are not uncommon, as, for example, in the cortex of many Magnoliaceae.

Among specialized forms of parenchyma cells we should also include the cells of the epidermis and endodermis and of the cork.

THE EPIDERMIS

The **epidermis** forms a continuous outer sheath over the exposed parts of plants, but in older parts it is usually replaced by the secondary bark. It is rarely more than one cell thick, except in tropical plants exposed to powerful sunlight. The cells are usually small and often of a rather flattened, tabular form (Fig. 443). They are living cells, but they very rarely contain chloroplasts. The inner walls may be thin or thick, but the lateral walls are thin and are usually provided with numerous large pits. Water can thus move easily through the epidermis from cell to cell, and it constitutes a first reserve from which water can be quickly mobilized to supply any area threatened by excessive evaporation. The lateral walls are also sometimes remarkably convoluted, as seen from above, forming a complex system of dovetailing whereby the cells are closely knit together (Fig. 444). The primary requirements of toughness and flexibility are thus ensured. This unique structure is probably due to rapid lateral expansion of the cells at a time when their outer walls are more rigid than their lateral walls.

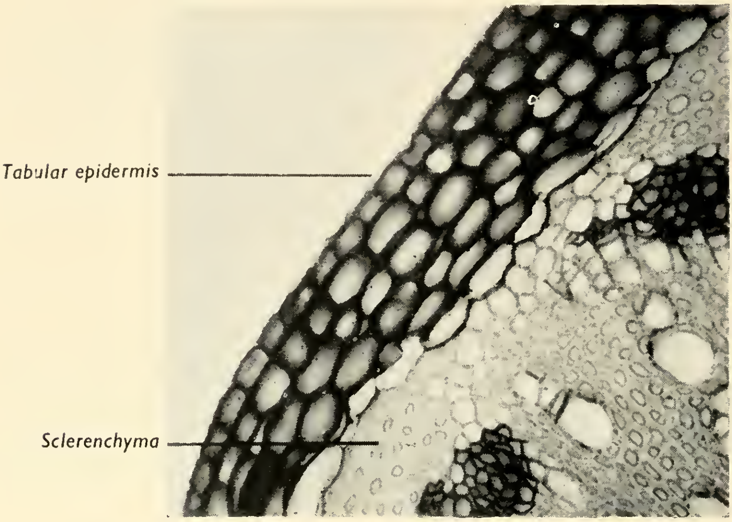

Fig. 443.—*Lysimachia punctata.* Tabular epidermal cells in stem.

Fig. 444.—*Carex pendula.* Superficial view of epidermal cells of leaf.

A true epidermis is essentially a protective layer, securing the inner tissues against desiccation. This function is associated with the deposit on the outer wall of an impervious layer of **cuticle,** which varies in thickness with the degree of exposure of the plant to a drying climate. In roots and in water plants it is non-existent, but it is found on the exposed parts of all land plants. It is especially thick in evergreens, while in a few desert plants it may reach such a thickness that it can be stripped off. Fruits, such as Apples, often have a heavy cuticle, and their keeping qualities largely depend on the retention of their moisture by this covering. The cuticle is very impervious to water, and if even a small portion be removed from an apple the rapid loss of weight which follows is striking evidence of its protective power. The cuticle is also important in resisting the penetration of parasitic Fungi or the sucking organs of insects, and the immunity of certain cultivated varieties to such attacks may sometimes be traced to the thickness of their cuticle.

The cuticle forms a continuous layer over the epidermis, closely moulded to the cell surfaces, so that, when isolated, it shows the pattern of the epidermal cells. It often bears fine ridges or papillae on the outer surface, which give it a velvety appearance. In plants where the epidermis persists for several years the cuticle is formed in successive layers, the outer being cracked and shed as new layers are formed beneath.

Cuticle is a complex mixture of fatty acids, partly free and partly combined with alcohols. They are mostly in a condensed condition and are in part saponified. It stains readily with fat-soluble dyes such as Sudan III. These fatty substances are apparently excreted through the outer walls of the epidermal cells, though the process is little understood. It also contains wax, and this may accumulate on the surface as a layer of minute granules or rods, which are the cause of the greyish " bloom " on many fruits and leaves, which are described botanically as **glaucous.** The Wax Palm, *Copernicia cerifera*, of Brazil produces such quantities on its leaves that it is collected commercially as Carnauba Wax.

Normally the cuticle is quite distinct from the epidermal cell walls, but in some cases these may become infiltrated with **cutin,** the name given to the cuticle substance, and are then said to be **cutinized** (Fig. 445). The cutinized cell wall may be much thicker than the cuticle itself. Walls which are cutinized may occur even in internal tissues, as in the coats of some seeds.

The epidermis is sometimes reinforced beneath by a second layer of cells, which may be cutinized or lignified. This is called the **hypodermis.**

THE ENDODERMIS

The **endodermis** is a single layer of cells surrounding the vascular tissues. It is formed by modification of the innermost layer of the cortical parenchyma. Typical endodermis is found in both stems, leaves and roots of Pteridophyta and in the roots of Spermatophyta, but in the stems of Spermatophyta it is often missing or is represented by a layer of cells with large starch grains.

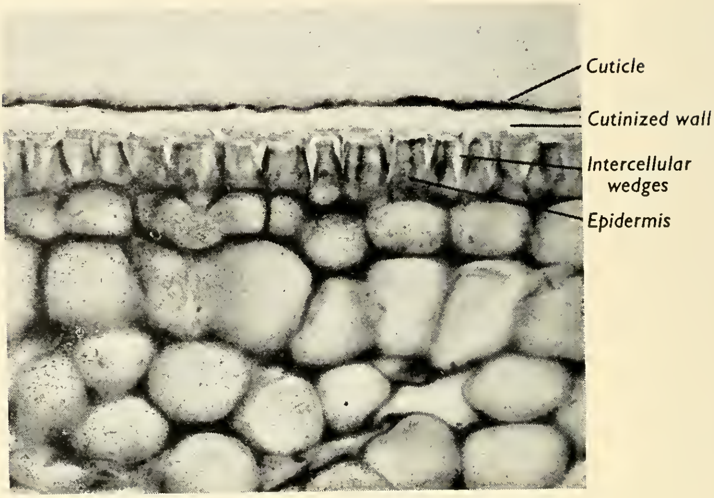

FIG. 445.—*Ficus elastica.* Transverse section of leaf showing cutinized epidermis.

There are two main types of endodermis, which are thin or thick walled. In both types the cells are somewhat elongated vertically and are at first thin walled. In the type common to Pteridophyta and most Dicotyledons the tangential walls remain thin, but a differentiated band forms on the radial walls, completely encircling the cells. This band, which is impregnated with lignin and with fatty acids, is called the **Casparian band** (Fig. 446). It is usually much narrower than the cell and appears in transverse sections as if it were a thickened zone on the radial walls, by which this type of endodermis is easily recognized. Broad Casparian bands are usually perforated by numerous pits.

The thick-walled type of endodermis, characteristic of monocotyledonous roots, is thickened with cutin, and sometimes partially lignified, either all over, or only on the inner tangential and radial walls. Such a layer is naturally impervious to water. Certain cells, however, called **passage cells,** remain unthickened (Fig. 446). They lie opposite the protoxylem cells (see p. 803). In cases where an endodermis becomes completely cutinized, as in old roots, the cortex is cut off from its water supply and disappears, leaving the endodermis as the external layer of the root.

THE CORK

Corky or suberized cells form the **phellem,** a thick layer of impervious cells which make up the outer bark of old stems and roots (Fig. 447). The cells appear square or oblong in outline and often rather narrow in transverse section, but in tangential view they usually show suturings like those of epidermal cells. The cell wall contains a definite layer of **suberin,** next to the middle lamella. Suberin is a mixture of fatty materials closely allied to cutin, and as a rule, only with difficulty distinguishable from it. Cutin and suberin differ chemically chiefly by the presence, in the latter only, of phellonic acid and glycerol. Some botanists restrict the term cutin to the material of the external cuticle and call all fatty wall materials elsewhere suberin, but others limit the latter term to the material found in the cork (Latin, *suber*). It is a matter of convention as there is no easy way of distinguishing them.

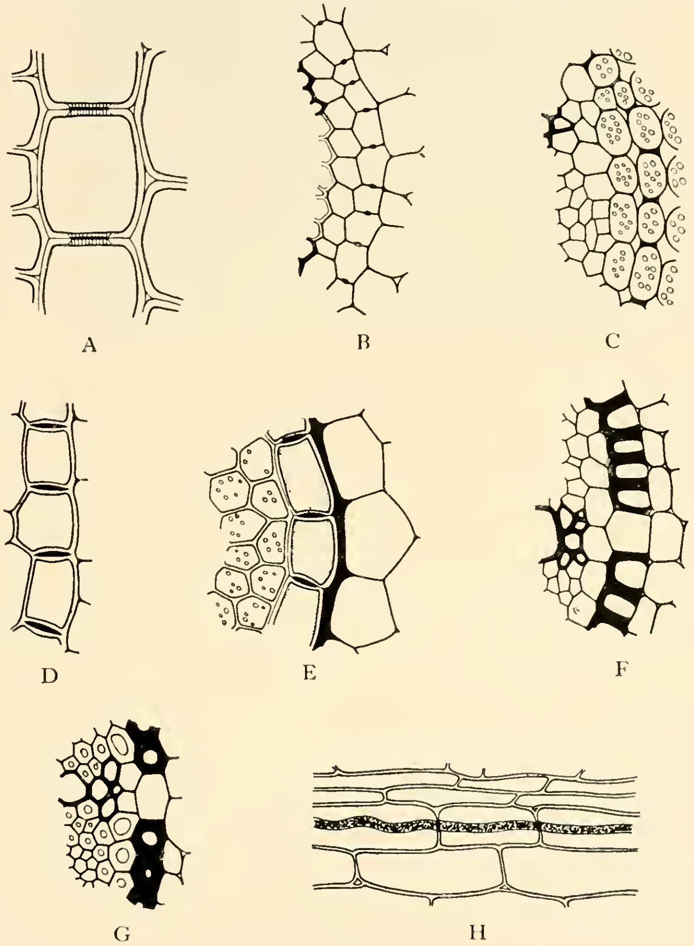

Fig. 446.—Types of endodermis. A, Diagram to show formation of Casparian band (*after Priestley*). B, *Ranunculus fluitans*. Stem (*after de Bary*). C, *Acorus calamus*. Root. D, *Dryopteris filix-mas*. Petiole, primary state (*after Priestley*). E, *Dryopteris filix-mas*. Petiole, secondary state (*after Priestley*). F, *Iris germanica*. Root. G, *Epidendrum sp.* Root. H, *Plantago major*. Leaf. Longitudinal aspect of Casparian band (*after Trapp*).

Physiologically suberization of the cell wall cuts off the water supply of the protoplasm and suberized cells thus soon die. Their walls remain, however, to build up the phellem tissue.

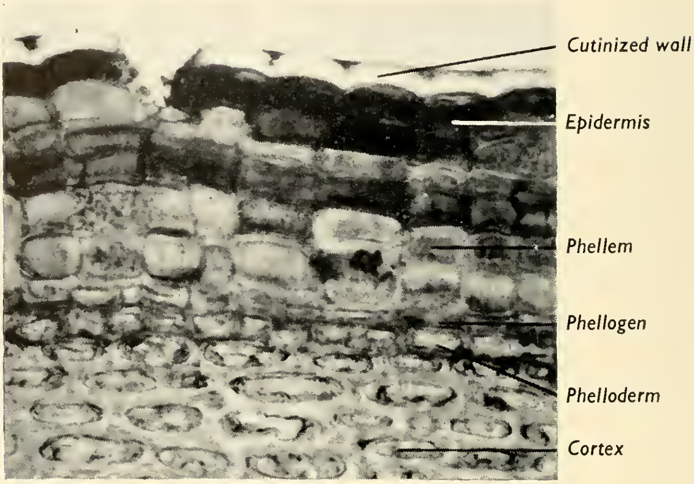

FIG. 447.—*Acer campestre.* Formation of cork in stem. For explanation of terms see p. 863.

Elementary Tissues: Prosenchymatous Types

These cells differ from the parenchymatous forms in being markedly elongated and having more or less pointed ends. The distinction is by no means clear-cut, but it has some value in designating at least two classes of cells, namely, fibre cells and conducting cells, which differ strikingly from any parenchymatous cell.

FIBRE CELLS

The typical **fibre cell** is narrow, very elongated and has long tapering points. The wall is highly thickened with concentric layers of cellulose usually impregnated with **lignin,** so that little internal space is left. In this wall are small pits, with pit canals running through the thickness of the wall to the cell lumen. The pits are circular in outline, but the canals are often expanded into narrow slits, which lie at an acute and constant angle to the cell axis. The slope of these slits in adjacent fibres is opposite, so that in longitudinal view they appear crossed within the circle of the pit outline.

Lignin is so important a substance that it is unfortunate that its chemistry is not yet fully known. It is the characteristic material of wood, and is hard, dense and relatively insoluble.

In spite of the efforts of many workers, the constitution of lignin is far from being satisfactorily settled. Indeed there is no certainty that lignin is really a homogeneous substance. Certainly a considerable chemical difference exists between the lignin in the cell wall and that in the middle lamella. The lignin of the cell wall contains 61 to 64 per cent. of Carbon and only 30 per cent. of Oxygen, so that it is not wholly carbohydrate, although it probably includes the sugar arabinose. Several workers have suggested a unit molecular weight between 800 and 900 for Spruce lignin and about twice as much for angiospermic lignin. The lignin of the middle lamella is denser and has a lower oxygen content. There is a considerable evidence for the existence of an aromatic or hydro-aromatic nucleus in the lignin molecule, perhaps related to coniferyl alcohol, and the colour reactions by which lignin is microscopically distinguished are attributed to this group. Similar colour reactions are given by many of the aromatic terpenes or "essential oils." No formula for lignin is yet possible as there is no agreement as to the molecular groupings or linkages present.

Lignification involves the impregnation of the cellulose wall with this mixture of substances, partially combined with the cellulose, but largely free, and usually results in thickening of the wall, with increased density and higher refractive index, *i.e.*, "brightness" under the microscope. It greatly strengthens and stiffens the cell wall, and in the case of fibres, at any rate, this is its primary value, as their function is entirely mechanical or skeletal. They are naturally therefore most developed in young organs, and particularly in Monocotyledons, where there is little wood. The strength of the wall is further increased by the presence of fine longitudinal rods of silica (Fig. 448).

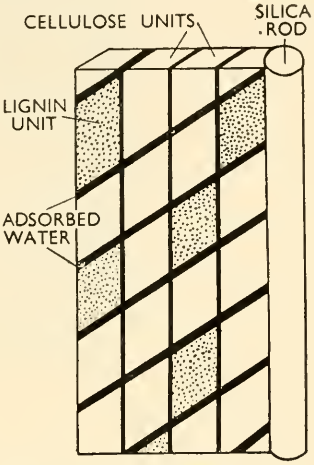

Fig. 448.—Diagram of sub-microscopic structure of the lignified wall of a tracheid. (*After Maby.*)

The tensile strength of lignin is remarkably high, in some cases nearly as high as that of steel, but it differs from metals in two mechanical respects, namely that its elastic extension is greater and that there is a much smaller interval between its limit of elasticity and its breaking point. A tissue which has been strained beyond its elastic limit is obviously permanently damaged and any further resistance to breakage would be valueless.

Cellulose is more elastic than either lignin or steel and therefore collenchyma allows for even greater stretching without damage than does lignified fibre ; hence it is especially valuable in flexible or ganslike petioles and young stems.

Occasionally fibres are found as isolated cells, and very striking examples may be seen in some leaves, as in *Camellia* or *Hakea*. They are not always pointed but may be columnar in form, and are called **sclereids** (Fig. 449).

Fibre cells are, however, usually found in bundles or masses called **sclerenchyma,** forming longitudinal strands, which are the material of many commercial fibres, such as jute, sisal and hemp. This solid, mechanical tissue is distributed in such a way as to give the maximum rigidity to the organs in which it occurs, and collectively it forms the **stereome** or supporting tissue of the plant (see Chapter XXI).

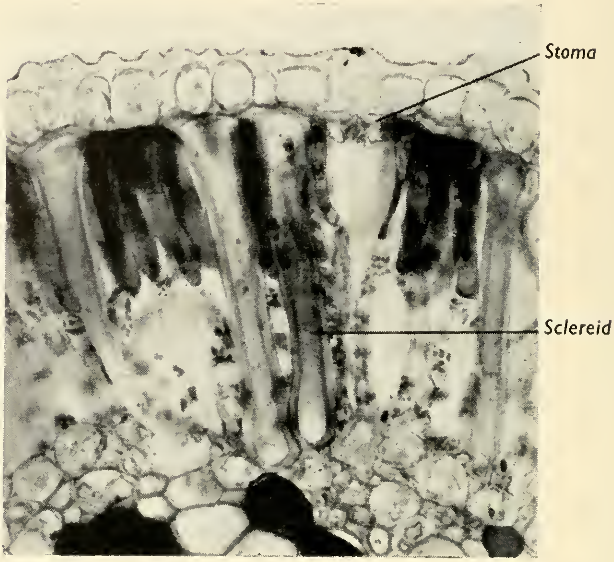

FIG. 449.—*Hakea pectinata*. Transverse section of leaf, showing sclereids.

The pointed ends of fibres in the sclerenchyma overlap considerably, and as this is not true of the cells from which they develop, it has been suggested that during elongation the points must push in between each other. This movement is called **sliding growth,** as the cell surfaces are assumed to slip on one another during the process. Its existence has not, however, been completely established. If it occurs it can only be of limited duration, particularly during the early amyloid stage of the cell wall, at the beginning of cell expansion. The maturation of the wall and of the middle lamella would probably soon put an end to such possibilities.

TRACHEIDS

Fibre cells are too narrow to be of any use for conducting liquids, and this is the principal function of the **tracheids** (Fig. 450), which make up a large part of what is generally called " wood." Tracheids are shorter and broader than fibre cells and their ends are less elongated, the taper being usually in two planes only, so that they are chisel-pointed. It is difficult to draw a sharp line between them and true fibres, and intermediate types or **fibre tracheids** are common. Tracheids are normally lignified, but the lignified material may be disposed on the wall in several different patterns. The thickness of the wall is much less than in fibres so that there is a large central lumen. The protoplasm disappears at maturity and only the wall remains.

The existence of a practically continuous series of forms connecting true tracheids with true fibres has led to much confusion in the anatomical description of woods. The tracheids which most resemble vessel elements (see below) are called vascular tracheids. They have the same kind of lignification as vessels and where they abut on vessels the pits between them are the same as those on the vessel. Tracheids which more resemble fibres are classed as fibre tracheids, though they may have the same kind of ring or spiral thickenings as vascular tracheids. The presence or absence of a border to the pits is often taken as a line of demarcation between tracheids as a class and true fibres, tracheids being defined as cells in which the pits to elements of the same type are bordered, while the fibres have only simple pits. This is not a precise boundary line, for the amount of bordering to a pit is very variable.

The best that can be said is that tracheids have definitely bordered pits, while the true fibre has usually simple pits, and is an elongated and commonly thick-walled cell, which in the sap wood often contains starch and is not infrequently transversely septate by thin cross walls, which are formed after the side walls have been thickened.

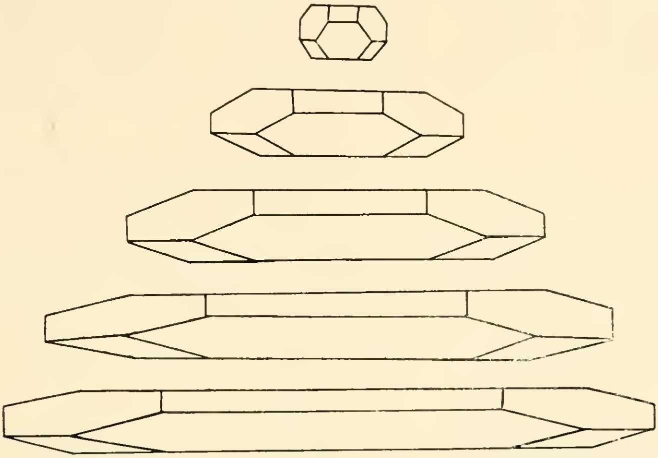

Fig. 450.—Growth of a tracheid from a cambial cell, showing progressive stretching due to vertical tension in the tissues. (*After Lewis.*)

The first tracheids to appear are differentiated very near the growing point, in the midst of cells which are actively expanding. A dead cell, such as a tracheid, is subject therefore to considerable lateral pressure from its neighbours and also to longitudinal strain from the elongation of the cells which are in contact with it. In such cells the lignified thickening takes either the form of transverse rings, or of one or more spirals round the cell, between which is the thin, cellulose wall (Fig. 451). This form of thickening is associated with the maximum of extensibility combined with considerable resistance to compression. These types are known as **annular** and **spiral** respectively, and they are characteristic of the first formed wood elements. Tracheids formed somewhat later show instead an anastomosing network of lignin bands and are called **reticulate**, while those developed in mature organs, where elongation has ceased, are called **pitted,** because the wall is fully lignified except for a number of pits. These may be either **simple pits,** as in parenchyma cells, or may be **bordered pits** (Fig. 452). In this latter case the pit membrane, *i.e.*, the primary wall, is roofed over on each side by

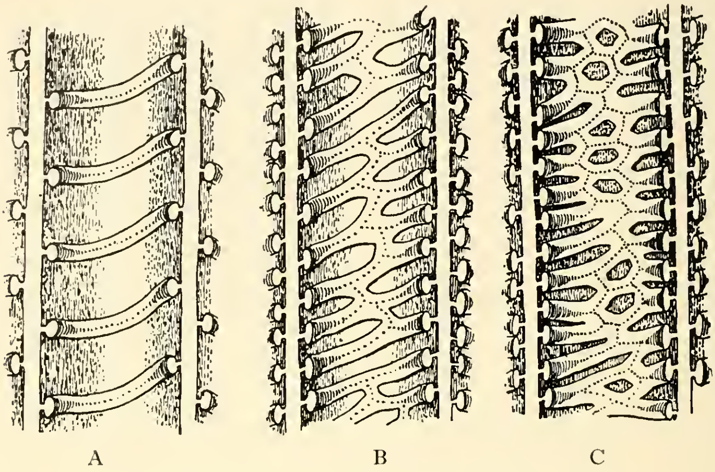

Fig. 451.—Types of tracheid wall thickening. A, Spiral. B, Reticulate. C, Pitted. (*After Zimmermann.*)

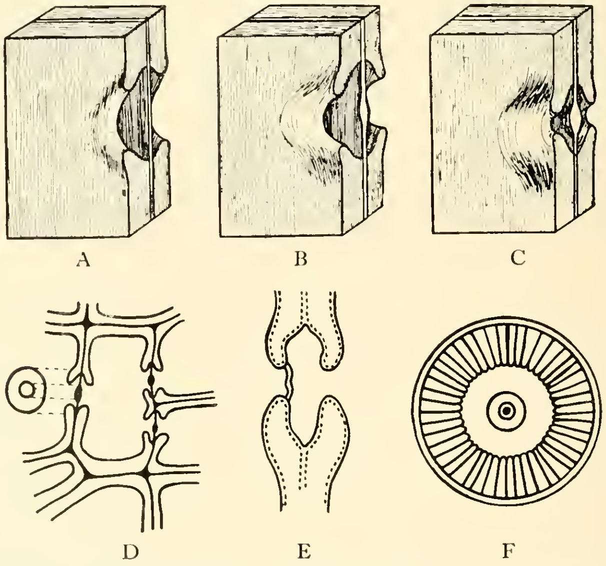

Fig. 452.—Bordered pits. A, B and C, Stages in the growth of border and torus in three-dimensional view. D, Bordered pits in transverse section. E, Bordered pit with torus displaced laterally, filling aperture of pit. F, Pit membrane in surface view with central torus and radial striations. (*After Stevens.*)

a dome of the lignified secondary wall. Each dome has a small opening at its apex giving entrance to the pit cavity. The pit membranes are very thin and are indeed sometimes perforate, so that fluids move very easily from tracheid to tracheid, even in these mature types. Frequently a small thickened disc, the **torus,** is formed in the centre of the membrane and in the highest type of bordered pit, as in *Pinus*, the membrane can be displaced from side to side, the torus exactly filling the opening in the dome, so that a valve action is secured. Bordered pits are characteristic of dead cells, such as tracheids, where there is no protoplasm to support the pit membrane.

One type of tracheid has narrow, transverse pits, like slits. This is called **scalariform,** from its likeness to the rungs of a ladder. It is the characteristic type in the Pteridophyta, but it also occurs in other groups.

VESSELS

Tracheids are individual cells, but where they are in contact end to end, the thin end walls may disappear, so that a chain of tracheids becomes an open tube, called a **vessel** or **trachea** (from its resemblance to the tracheae of insects) (Fig. 453). Vessels are almost confined to the Angiosperms, where they make up an important part of the wood. If they are well developed they practically supersede the tracheids for the conduction of water, and the latter then function simply as water stores, and may be limited in number to a few around the vessels. The cellular units which make up a vessel are called the **vessel elements.**

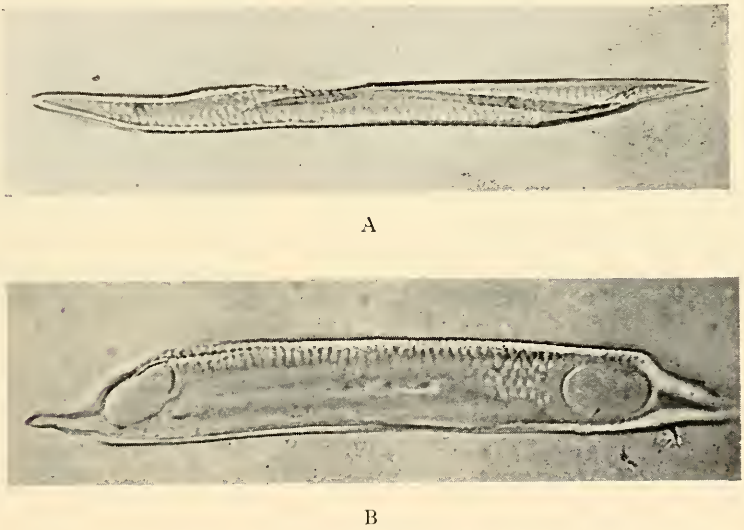

FIG. 453.—*Ulmus procera.* Comparison of tracheid and vessel element. A, Pitted tracheid. B, Pitted vessel element showing sub-terminal pores. Isolated by maceration.

Among the arboreal Dicotyledons (which includes most of our forest trees) the end walls of the elements are very oblique and are partly lignified, so that the formation of vessels involves only the solution of the pit membranes between the bars of lignin. In herbaceous plants, however, the vessels are usually broader and their elements become united before their differentiation is complete. The cell elements involved are often very short and the end walls transverse and unthickened, so that they disappear completely, leaving at most a trace of the rim (Fig. 454). This usually happens before the protoplasm of the individual cells has disintegrated.

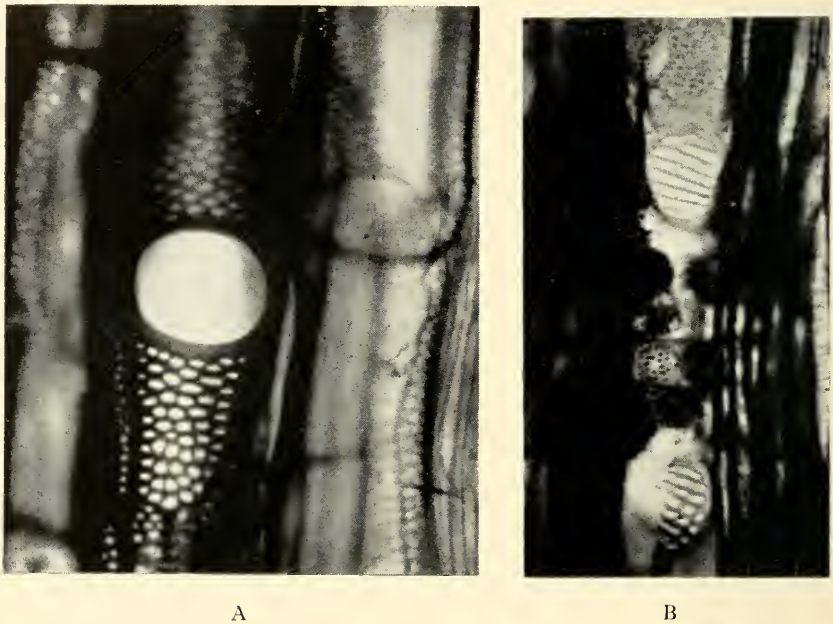

FIG. 454.—Comparison of terminal perforations in vessel elements. A, *Helianthus annuus*. Open pore. B, *Salix caprea*. Scalariform end walls.

Vessels show the same types of differentiation in wall thickening that are found in tracheids. In addition, however, large vessels show a coarse network of markings, due to contacts with the walls of smaller adjacent tracheids.

Vessels are not of indefinite length. In certain trees they may be many feet long, perhaps even the whole length of the trunk, but the average length is much less, probably less than 3 ft. Usually the vessels are considerably wider than other elements of the wood, though exceptions occur, as in the very fine-grained wood of *Buxus* (Box), which gets its name from the German *Buchs*, on account of its use in making wood-cuts for illustrations. Climbers, especially the woody climbers or lianas of the tropics, have notably large vessels, sometimes more than 1 mm. across, which is associated with the great length of their stems.

Xylem Parenchyma

Apart from tracheids and vessels the woody tissue contains numbers of short lignified cells usually called **xylem parenchyma.** This term, **xylem,** covers the aggregate of woody vascular tissues, and we shall meet it constantly henceforth. The xylem parenchyma have very numerous simple pits. They may be either dead or living, and in the latter case may contain stored starch. They occur in three different ways in different woods. They may be generally distributed among the other elements, they may be grouped around the vessels or they may be formed along with the last xylem cells produced at the end of the growing season. The type of distribution is helpful in identifying species of timbers.

Sieve Tubes

The non-lignified prosenchyma constitutes another type of vascular tissue. The chief example is the **sieve tube.** Sieve tubes are longitudinal files of elongated, thin-walled cells, the transverse walls between them being pierced by numerous pores, which gives them the name of **sieve plates.**

In its early state a sieve tube element is a typical living cell, with protoplasm showing cyclosis, but during development the movement ceases, the nucleus disappears, the cytoplasm becomes coarse and permeable, the distinction between vacuole and utricle becomes blurred, and probably the mature cell eventually dies. The vacuole contains a strand of slime, which often appears to be accumulated at the sieve plates into the so-called **slime plugs.** These plugs are probably only artificial appearances and are not seen in uninjured cells.

The pores of the sieve plate are really open perforations through which the protoplasm of neighbouring elements makes direct contact. They are therefore extremely large plasmodesma. Whether the slime also passes through the pores is still uncertain, but there can be no doubt that the sap can pass freely through the highly permeable protoplasm. The mature sieve plate has usually linings to the pores formed of a polysaccharide substance called **callose,** which gradually increases in amount until it forms a thick pad over the plate. The protoplasmic connections persist through the pad for some time, but are eventually broken. Such pads may form during the first winter and be dissolved in spring, but in such cases the second winter brings the formation of a permanent pad and the end of the tube's functional life. **Sieve fields,** similar in structure to the sieve plates, may often occur on the side walls of the tube where it is contiguous with another sieve tube (Fig. 455). Sieve tubes do not serve simply for the passage of water as such but are conductors of carbohydrates and nitrogenous food materials.

Associated with each sieve tube is a **companion cell,** which is derived by division from the same mother cell as the sieve tube element alongside which it lies. It is much narrower than the sieve tube and has a nucleus and abundant cytoplasm. The wall between it and the sieve tube has numerous simple pits but no pores.

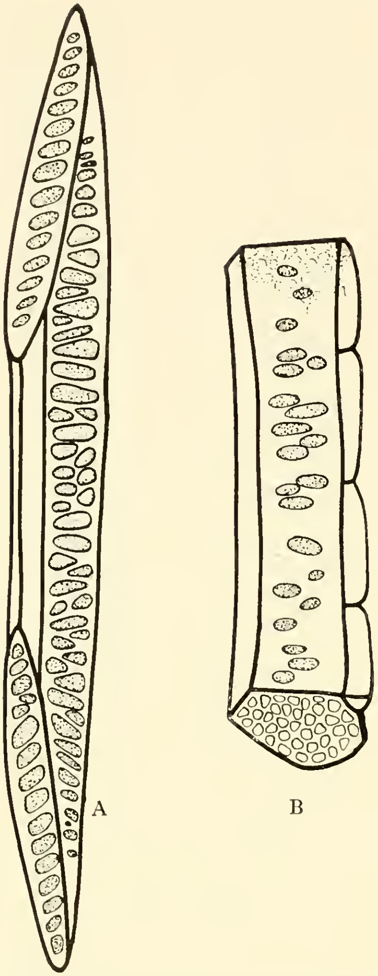

Fig. 455.—Comparison of sieve tube elements. A, *Juglans nigra*, with multiple sieve plates on oblique end walls. B, *Robinia pseudacacia*, with simple transverse sieve plates. Both types also show lateral sieve fields. (*After Eames and McDaniel.*)

Phloem Parenchyma

Like the vessels, the sieve tubes are constantly associated with thin-walled parenchyma cells, which, unlike the companion cells, are often filled with starch. This is called the **phloem parenchyma.** The tissue formed of sieve tubes, companion cells and phloem parenchyma is called collectively the **phloem,** which together with the lignified **xylem** form the **vascular tissue.**

Cambium

Lastly we must mention a type of meristematic tissue which has the special function of producing the vascular elements, both lignified and non-lignified. This is the **cambium.** It is a direct downward continuation of the apical meristem, but its cells have a peculiar, prosenchymatous shape. In transverse section they are narrowly rectangular, the longer diameter of the rectangle always lying tangentially to the axis of the plant. Vertically they are chisel-ended, like the tracheids, the points alternating to the right and left sides (Fig. 456). Like other meristematic cells they have thin walls, the radial walls being the thickest.

Epidermal Outgrowths

Epidermal cells give rise to a variety of specialized outgrowths grouped under the general name of **trichomes,** which includes all kinds of hairs and structures derived from hairs (Fig. 457).

The simplest kind of hair is a unicellular, tubular outgrowth from a single epidermal cell. If it is very short it may be no more than a **papilla.**

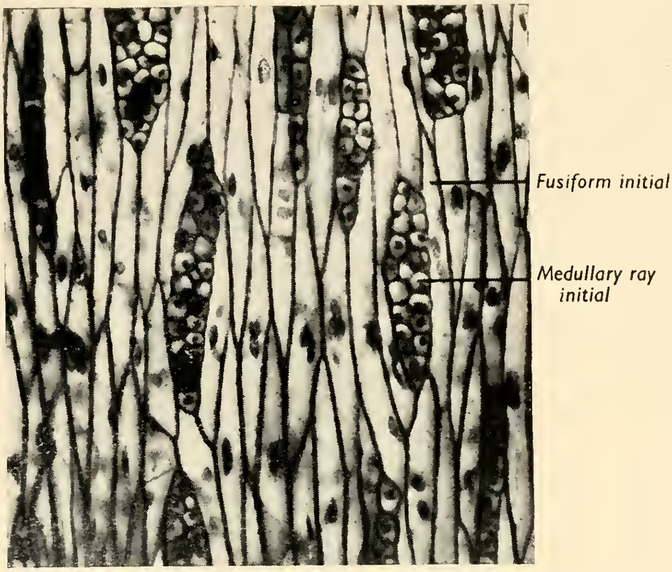

FIG. 456.—*Ulmus procera*. Tangential view of the cambium in a woody stem, showing elongated cambial elements and embryonic medullary rays.

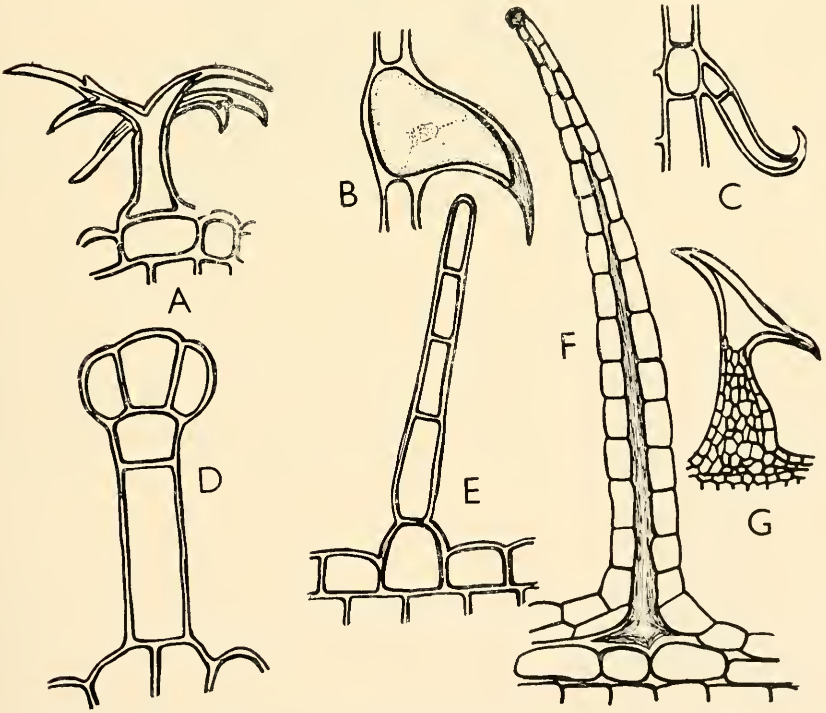

FIG. 457.—Types of trichomes. A, *Lavandula vera*. Branched hair. B, *Galium aparine*. Climbing hair. C, *Phaseolus multiflorus*. Hooked hair. D, *Primula sp.* Multicellular glandular hair. E, *Calophyllum sp.* Multicellular hair. F, *Begonia imperialis*. Multicellular hair with internal sclereid. G, *Humulus lupulus*. Grapnel hair.

Papillate surfaces are usually velvety in texture. If hairs are scanty the surface is called **hispid,** while if they are numerous they form a woolly or **tomentose** surface. If they are absent the surface is called **glabrous.**

The more advanced types of hairs are multicellular and, like the unicellular types, they may be simple or branched. The branching is often complex and gives rise to a multitude of varied forms. The branches sometimes become closely interlaced so that the epidermal surface is quite hidden from view. Dense coverings of hairs are traditionally reputed to protect leaves against excessive evaporation, but experiment does not altogether support this idea. For root hairs see Chapter XX.

Hairs may also be formed by the combined outgrowth of a group of epidermal cells. Such hairs commonly form secretory glands (see below). Sometimes, however, they become woody and comparatively massive, and are then known as **prickles** (Fig. 458). The Rose and the Blackberry provide good examples. Unlike true thorns (see Chapter XXI) they are purely epidermal structures and usually contain no vascular tissues (Fig. 459). Moreover, they may occur anywhere on the plant, on stems, leaves, or even, rarely, on roots or flowers. Hairs may also be flattened into **scales,** closely covering exposed surfaces.

FIG. 458.—*Rosa sp.* showing stem prickles.

GLANDS

Glands are classified physiologically as either **secretory** or **excretory,** but it is difficult to draw a clear line between the two functions. Broadly speaking a secretion is directly valuable to the plant and an excretion is a superfluous or deleterious substance. Plants have no regular method of evacuating their excretions as animals have. They dispose of them internally, building them into their structure, usually in superannuated

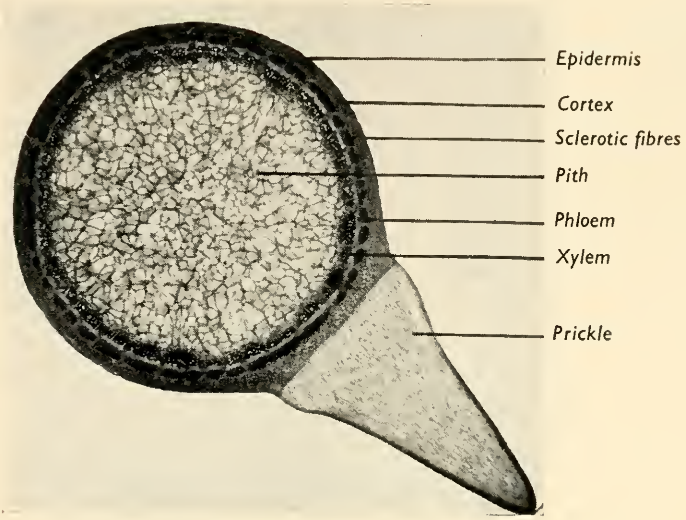

FIG. 459.—*Rosa sp.* Transverse section of stem passing through base of prickle showing its superficial origin.

tissues. Thus they may sometimes become indirectly useful to the plant. For example, mineral materials may serve to strengthen tissues. Again, the aromatic terpenes, to which plant odours are due, are superfluous substances from the point of view of metabolism, but they serve an essential biological purpose in attracting insects to flowers, whereby pollination is effected.

From the anatomical standpoint it is simpler to classify glands as either superficial or internal. The superficial glands are usually modified hairs in which one or more cells contain the secreted material. A gland of this type is the stinging hair of the Nettle (*Urtica dioica*) (Fig. 460). The secretory cell is flask-shaped, the bottom of which is seated on a pedestal of small cells. The neck is drawn out into a long, tapering cone, the wall of which is impregnated with Calcium carbonate, and the tip is bent sideways and forms a small silicified bulb. When touched this bulb breaks off, leaving a sharp point, with a lateral opening like a hypodermal needle, which pierces the skin. Pressure forces the poison upwards from the flask-like base of the cell and into the subcutaneous tissues. The gland contains a mixture of histamine and acetyl

FIG. 460.—*Urtica dioica.* Stinging hair showing pedestal of small cells, flask-shaped secretory cell with long neck and terminal bulb.

choline. The former causes itching and the combination produces the prolonged burning sensation. Acetyl choline alone is without effect. *Urtica stimulans*, the Java Nettle, causes serious illness, comparable in severity to a snake bite.

The glands produced on the leaves of the Insectivorous Plants are generally glandular hairs and they function both for the capture and the digestion of the insect prey. They will be discussed in detail under Bionomics in Volume IV.

Superficial glands, if not formed from hairs, may be simply modified patches of epidermis, as, for instance, in the **nectaries,** found in most flowers and sometimes also on leaves or stems, where they are called **extra-floral nectaries** (Fig. 461). The epidermis of these gland areas has no cuticle and consists of a layer of narrow, highly protoplasmic cells called **epithem.**

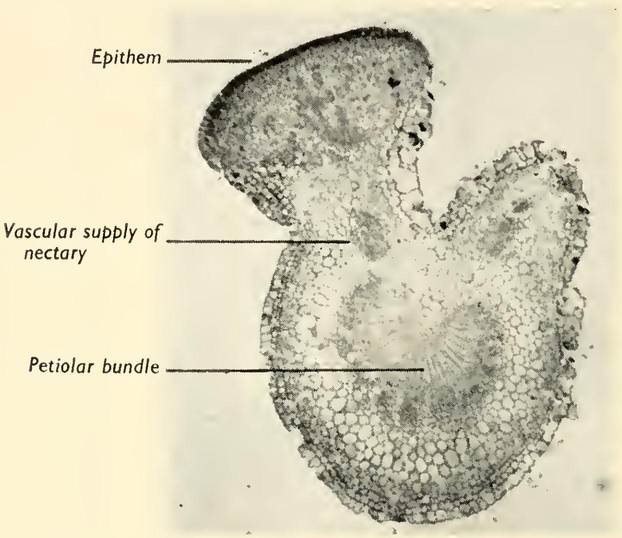

Fig. 461.—*Prunus cerasus.* Garden hybrid. Transverse section of petiole showing two extra-floral nectaries, the one on the right cut obliquely.

A peculiar type of gland, associated with the excretion of water, is that called a **hydathode.** These are usually modified stomata permanently open and supplied beneath with a strand of vascular cells ending in a group of epithem cells (Fig. 462). They are often to be found at leaf margins, where, in moist weather, the drops of excreted water may be seen hanging.

Internal glands may be simply cavities in the tissues. They originate in two ways. Firstly, by the dissolution of cells, leaving a space in which the secretion accumulates. These are known as **lysigenous,** and they have usually ragged remains of cells lining the cavity (Fig. 463). Secondly, by the separation of cells, through solution of the middle lamella. In this case the space is usually more regular in form. Such glands are called **schizogenous.** The surrounding cells divide tangentially to produce a special layer of small cells round the internal cavity. These are the secretory cells and they constitute the **epithelium** (Fig. 464).

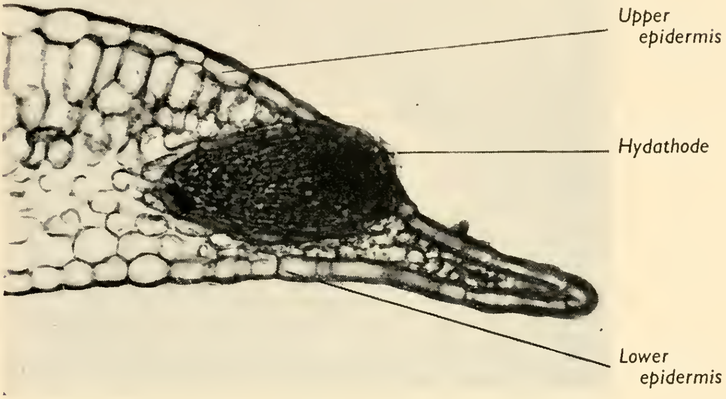

FIG. 462.—*Saxifraga sp.* Transverse section through leaf margin showing hydathode gland.

Lysigenous glands are usually more or less spherical. Many of the perfume glands in flowers and leaves are of this type. Schizogenous glands may also be spherical, but they are more often elongated into secretory sacs, or even into long canals, branching and anastomosing through the whole plant. This kind of gland frequently contains terpenes, or " essential oils "

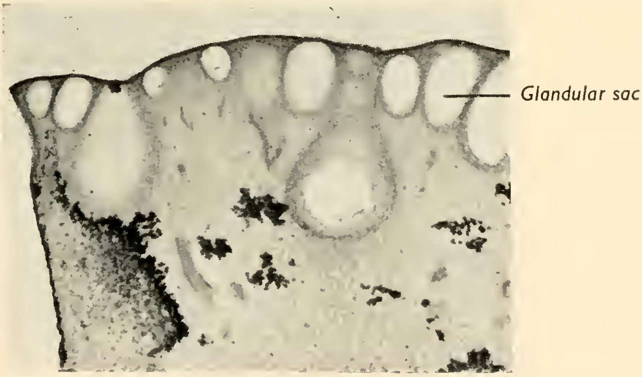

FIG. 463.—*Citrus limonum.* Section through pericarp of fruit, showing large lysigenous secretory sacs covered only by epidermis and containing essential oil.

as they are called, for example, turpentine in the Pines ; or they may produce mucilage, another common secretion.

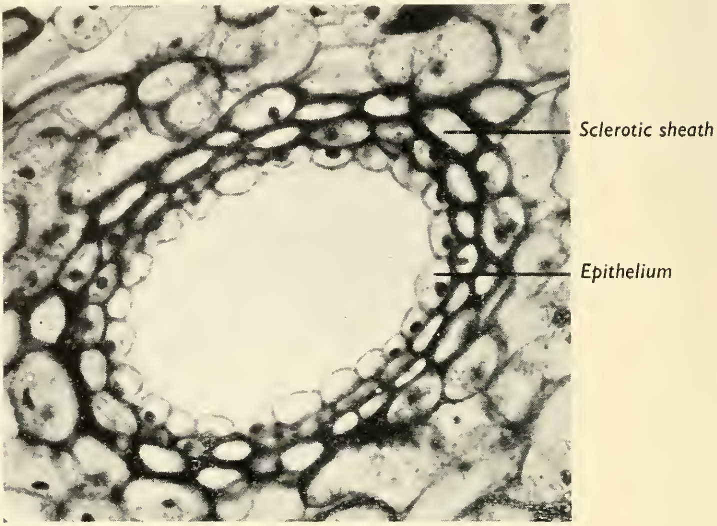

Fig. 464.—*Pinus sylvestris.* Transverse section of schizogenous resin canal with lining epithelium and sclerotic sheath.

Fig. 465.—*Euphorbia splendens.* Latex tubes in stem cortex.

A peculiar type of internal secretion is that known as **latex.** This is also formed in extensive canal systems throughout the tissues of those plants in which it occurs, but these canals are not intercellular spaces but are greatly elongated cells, inside which the secretion is formed (Fig. 465). Frequently they form by the junction of numerous cells together, when they are called **latex vessels.** Alternatively **latex tubes** are formed by the enormously extended growth of a single cell, first distinguishable in the embryo plant, which ramifies through all the tissues, continuing to grow and branch as long as the plant lives. Latex tubes have smooth cellulose walls, but latex vessels have rough walls due to the breakdown of the component cells.

Latex itself is a complex emulsion, made up of droplets of many substances—resin, tannin, oils, proteins, wax, etc.—dispersed in a watery medium. In the Euphorbiaceae starch grains of a peculiar dumb-bell shape are also included (Fig. 466). Most important, however, is the hydrocarbon substance called **caoutchouc,** one of the polyterpenes, which is the mother substance of rubber. It is generally present in latex, but only in a few cases in sufficient amount to be commercially valuable. (See Volume IV, under Rubber in "Economic Botany.")

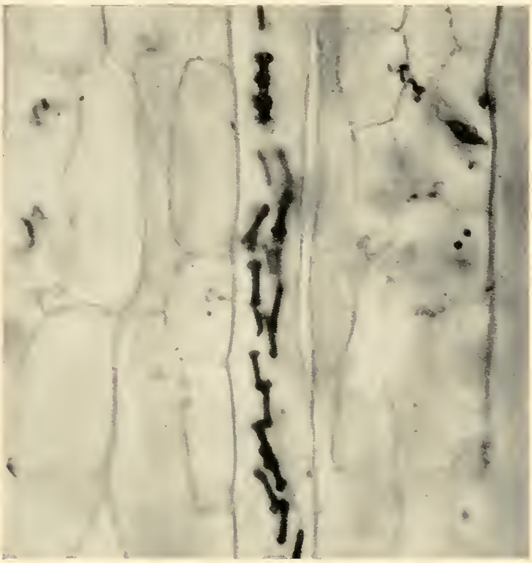

Fig. 466.—*Euphorbia splendens.* Latex tube showing thickened walls and dumb-bell shaped starch grains.

Special Cell Contents

In studying Plant Histology, cells will often be noticed which contain special substances deposited in them, substances which, unlike the reserve foods such as starch, oil and protein, are not directly concerned with the life of the cell.

Prominent among such special cells are those containing **tannin,** in brown amorphous masses. These are usually dead cells in old pith or bark tissues, but the tannin so deposited is previously to be found dissolved in the cell-sap of many cells which are still living.

Crystals are also of frequent occurrence in cells (Fig. 467). The principal substance which forms these crystals is **Calcium oxalate.** It may form large, solitary rhombohedra or crystals twinned in various ways. One frequent type is the **cluster crystal,** a spherical aggregate with points radiating out all round it. Another form, commonest in Monocotyledons, consists of a sheaf of fine needles, which are called **raphides.**

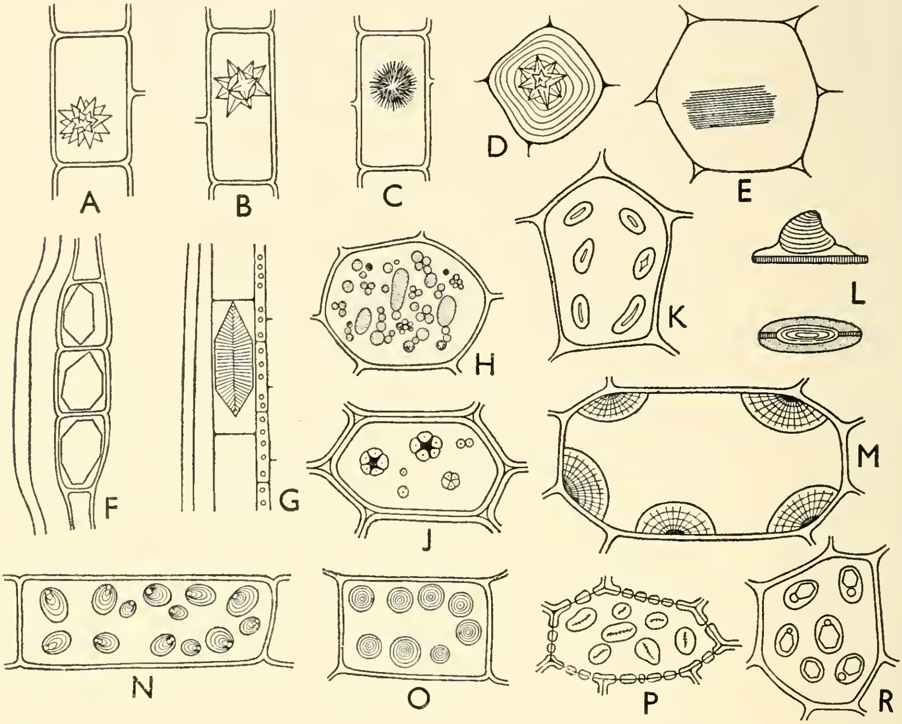

FIG. 467.—Types of cell crystals of Calcium oxalate: A, *Carica papaya.* Cluster crystal in cortical cell. B, *Juglans nigra.* Cluster crystal with organic centre in phloem parenchyma. C, *Viburnum lentago.* Cluster crystal in cortical cell. D, *Carya glabra.* Cluster crystal embedded in stone cell. E, *Smilacina racemosa.* Bundle of raphides in pulp cell of fruit. F, *Juglans nigra.* Rhombohedral crystals in wood parenchyma. G, *Tilia americana.* Rhombohedral crystal in phloem parenchyma. Types of reserve substances: H, *Fragaria sp.* Starch grains in pith cells. J, *Pisum sativum.* Compound grains in cell of cotyledon characteristic of wrinkled seeds. K, *Alsophila sp.* Starch grains in pith cells. L, *Phajus grandiflorus.* Formation of starch grain in plastid. M, *Dahlia variabilis.* Sphaero crystals of inulin. N, *Solanum tuberosum.* Starch grains in underground stem. Eccentric type. O, *Triticum vulgare.* Starch grain in endosperm. Centric type. P, *Phaseolus multiflorus.* Starch grains in cotyledon. R, *Ricinus communis.* Aleurone grains in endosperm. (*From various sources.*)

In the leaves of the Urticaceae and their allies there often occur certain enlarged cells, called **idioblasts,** in which crystalline aggregates of **Calcium carbonate** are deposited on a cellulose peg, which projects from the cell wall. These **cystoliths** may fill the whole cell (Fig. 468).

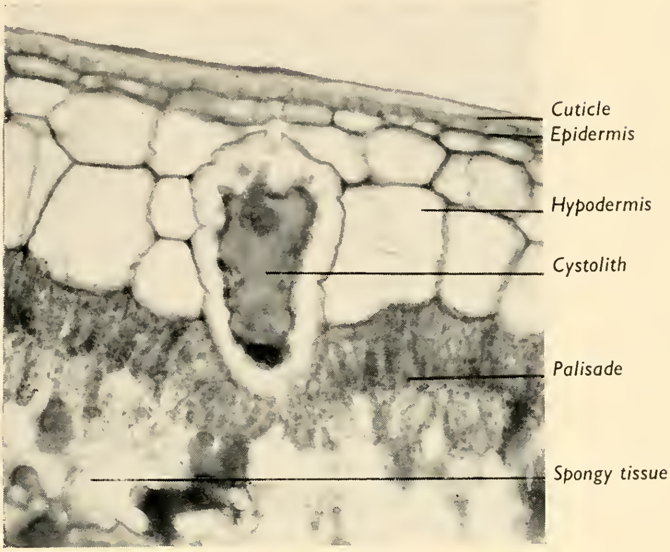

FIG. 468.—*Ficus elastica.* Transverse section of leaf showing cystolith in idioblast cell with supporting cellulose peg.

Tissue Culture

As we pointed out at the beginning of this chapter that the plant cell retains its potentiality for regeneration, even when mature, it will easily be grasped that the cultivation of isolated tissues is not possible with plants, as is the case in animals. Small groups of plant cells, if isolated, either die or proceed to develop and differentiate, to regenerate either a complete plant or a complete organ. They do not simply multiply their own kind of cell as do those of animal tissues. This power of regeneration is so great in some plants that a new individual can be raised from even a very small portion of tissue. In the extreme case of *Begonia phyllomaniaca* it has been achieved from a single hair. Isolated root tips have been subject to much experimentation. They usually regenerate complete root systems, without any shoots or leaves, and if given suitable nutrition, including Vitamins B_2 and B_6, they may apparently continue indefinitely in their isolated growth.

CHAPTER XIV

THE PTERIDOPHYTA: FILICALES, THE FERNS

THE phylum Pteridophyta includes those plants which are sometimes called the **Vascular Cryptogams.** The term Cryptogam is an old name which covers all the non-flowering plants, in which, at one time, the sexual reproduction was unknown. The epithet " vascular " distinguishes the Pteridophyta from the Bryophyta and other lower groups, in which no true xylem is formed. Furthermore this group shows the same morphological division of the body into stem, leaf and root which is characteristic of the higher group, the Flowering Plants. In the Bryophyta, it will be remembered, there may be stems with leaves, but there are no roots.

The Pteridophyta includes not only a large number of present-day genera, but also a great many fossil types. In fact the modern species are considered to represent only the remains of what was once a far more important group, and it seems probable that in the late Devonian and Carboniferous geological periods they made up a considerable part of the vegetation. Many of the genera which at the present day are quite small plants are descended from ancient groups which, in their day, formed large trees. *Lycopodium* and *Equisetum*, which to-day seldom reach more than a foot or two in height, are the remains of a group which in the Coal Measures produced extensive forests. In more recent times these Coal Measure plants have been succeeded by the Spermatophyta or Flowering Plants, which have relegated the Pteridophyta to a subordinate position in the world's flora.

The members of the Pteridophyta vary very greatly in form, and we can distinguish two main evolutionary tendencies. One resulted in the production of large leaves and relatively small stems, which are collectively spoken of as the **megaphyllous types,** and are represented by the Ferns; and the second, in which the leaves are small in relation to the stem, which are called the **microphyllous types,** represented by the Club Mosses and the Horse-tails.

The anatomy of these plants is to some extent dependent upon the type of leaf which they bear, but in all of them the stem is divided into an outer **cortex,** which is composed of parenchyma, together with, generally, a certain amount of sclerenchyma, and a central conducting system or **stele.** This latter structure contains the xylem and phloem, together with certain other types of cells. A similar, though generally simpler, structure is found in the roots. The leaves in megaphyllous types consist of leaf stalk or **petiole** and a flat blade or **lamina.** Branches of the stele, or **leaf traces,** pass out along the petiole and thence by further ramification into the lamina, forming the " veins." Microphyllous leaves are much simpler, with no petiole and usually only one vein.

The reproductive organs are generally borne either on the leaves or in the axils between the leaves and the stem. They consist of little capsules called **sporangia,** in which **spores** are developed. These spores may be all of the same size, when the plant is said to be **homosporous,** or they may be of two different sizes and the plant is then spoken of as **heterosporous.** In the heterosporous types the smaller spores are termed **microspores** and are developed in **microsporangia,** while the larger spores, which are generally produced in smaller numbers, are termed **megaspores,** and are formed in **megasporangia.**

From the fact that the members of the Pteridophyta produce spores we realise that they represent sporophytes, being comparable with the sporogonium of the Bryophyta. The spores on germination give rise to the gametophyte plants, which are usually small, insignificant structures, sometimes living an independent life and assimilating food material for themselves, but often living enclosed within the spores or else saprophytically underground. We see, therefore, that one of the most characteristic features of the Pteridophyta is that the sporophyte has become the dominant part of the life-cycle while the gametophyte has been much reduced. For this reason we must be careful not to compare, for example, the Fern plant with the Moss plant, since they belong to opposite parts of the cycle of alternation of sporophyte and gametophyte.

CLASSIFICATION

The classification of the Pteridophyta is somewhat complicated and elaborate, for in considering the various groups which comprise this assemblage of plants we must take into consideration the many and varied fossil forms which are no longer represented in the present-day flora. These we shall consider later, in Volume III.

It is, however, impossible to give a clear classification of the group without reference to these fossil types, and the following scheme is an outline of an inclusive arrangement :—

A. **PSILOPSIDA.**
  1. **Psilotales,** *e.g.*, *Psilotum.*
  2. **Psilophytales,** *e.g.*, *Rhynia*, *Asteroxylon* (fossils).

B. **LYCOPSIDA.**
  1. **Lycopodiales,** *e.g.*, *Lycopodium*, *Selaginella*, *Lepidodendron* (fossil).
  2. **Isoetales,** *e.g.*, *Isoetes.*

C. **SPHENOPSIDA.**
  1. **Equisetales,** *e.g.*, *Equisetum*, *Calamites* (fossil).
  2. **Sphenophyllales,** *e.g.*, *Sphenophyllum* (fossil).

D. **PTEROPSIDA.**
  Filicales, e.g., *Dryopteris*, *Pteridium*, *Osmunda*, *Hymenophyllum*, *Marattia*, *Botrychium*, *Azolla.*

Although this arrangement probably represents the phylogenetic sequence of types, we shall consider the Pteropsida first because, although the anatomy of the Filicales is the most complicated, they illustrate best the alternation of generations characteristic of the Pteridophyta and are therefore usually selected for junior study.

PTEROPSIDA *

The Pteropsida are distinguished from the other groups of the Pteridophyta by their megaphyllous habit, that is to say, their leaves are normally large in relation to the size of the stem, and the leaves rather than the stems are the dominant feature of the plant's architecture. Along with this morphological difference goes the anatomical character that in most cases the stele in the stem of adult plants shows **leaf gaps,** where the leaf traces are given off. This character is naturally absent or very slightly developed in stems with solid steles, and even in other cases it is subject to much variation according to the relative size of the leaves. Nevertheless, it is so widespread in the group, occurring even in very reduced forms, that it must be considered to be a distinguishing group character.

FILICALES

There is only a single order, the Filicales, and they therefore exhibit the same general characters as those already enumerated for the Pteropsida. Since it will be necessary for us to consider a number of examples of this order, on account of their marked differences, it is desirable to go somewhat more fully into the classification of the Filicales which we shall describe in this chapter.

Eusporangiatae.

Homosporous. Sporangia developing from a group of cells; the sporangial wall consisting of several layers of cells.

Marattiaceae, *e.g.*, *Marattia.*
Ophioglossaceae, *e.g.*, *Botrychium.*

Leptosporangiatae.

Homosporous. Sporangia developing from a single epidermal cell; the mature sporangium wall consisting of a single layer of cells.

Osmundaceae, *e.g.*, *Osmunda.*
Hymenophyllaceae, *e.g.*, *Hymenophyllum.*
Polypodiaceae, *e.g.*, *Dryopteris*, *Pteridium.*

Hydropteridae.

Heterosporous. Sporangia enclosed within a modified leaf segment or a closed indusium.

Salviniaceae, *e.g.*, *Azolla.*

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* Used here in a restricted sense to cover the megaphyllous Pteridophyta only. For the wider application of the term by Jeffrey see p. 649.

Bower has arranged the Ferns in three biological groups, on the basis of the order in which the sporangia develop. He distinguishes three types :—

1. *Simplices.* All sporangia in a sorus develop simultaneously. This type is more characteristic of Palaeozoic Ferns than of living genera, but it is shown by the Eusporangiatae and by the Osmundaceae and one or two related families.
2. *Gradatae.* Sporangia develop in succession from the apex to the base of the elongated sorus. Examples : Hymenophyllaceae, Salviniaceae.
3. *Mixtae.* Sporangia develop in the sorus without any fixed order. Example : Polypodiaceae.

It must be understood that this is simply a biological grouping and it is not to be taken as offering an alternative classification, for some families may have genera in more than one group.

In similar fashion Bower has distinguished two series of Ferns which differ in the position of their sporangia on the leaf. These are the *Marginales*, in which the sporangia are attached at the leaf margin, *e.g.*, *Hymenophyllum* and *Pteridium* ; and the *Superficiales*, in which the sporangia are on the lower leaf surface, *e.g.*, *Marattia*.

We have chosen to begin our description of the Filicales with the type *Dryopteris filix-mas*, the Male Fern, in order that the junior student may familiarize himself with the characteristics of this standard type before passing on to those other types which are usually the subjects of more advanced study.

Leptosporangiatae : Polypodiaceae

The Polypodiaceae are characterized by the annulus of the sporangium, which is vertical, that is, it lies in the same plane as the sporangial stalk. It is incomplete and does not surround the whole sporangium, which dehisces transversely. The family is very large and widely distributed and its members are mostly herbaceous with erect root stocks or creeping rhizomes.

Dryopteris filix-mas (The Male Fern)

The Male Fern occurs commonly in woods and hedgerows (Fig. 469). It possesses a short, blunt, unbranched stem, which grows obliquely upwards through the soil and appears but little above the surface. It increases in diameter with age, so that the top is broader than the lower end, like a carrot. It varies considerably in size, but is seldom more than a foot in length, and appears to be about 4 or 5 in. in diameter, though in reality it is considerably narrower, since the stem is completely covered by the persistent bases of the old leaves, on which adventitious buds sometimes develop and may produce an appearance of branching.

Compared with some of the Tree Ferns which are found in the tropics and in New Zealand the stem of the Male Fern is insignificant, for the Tree Ferns may reach a height of 60 ft., with a trunk as much as 2 ft. in diameter (Fig. 470).

FIG. 469.—*Dryopteris filix-mas.* Full-grown plant. Much reduced.

FIG. 470.—*Dicksonia sp.* Tree ferns at Caerhays Castle, Cornwall.

Reproduced from a photograph by Mr R. A. Malby, from the "Journal of the Royal Horticultural Society."

The leaves, which are usually spoken of as **fronds,** may be from 1 to 3 ft. in length and are much divided. A divided leaf of this kind is termed a **compound leaf,** and is composed of a number of separate **leaflets,** which in the Male Fern are called **pinnae.** These are again subdivided into **pinnules.** The pinnae are borne on a main stalk or **rachis,** which is a continuation of the petiole. In the young state both the petiole and rachis are clothed with dry, brown scales or **ramenta.**

The leaf takes two years to mature, and in their first year both the petiole and the rachis are coiled up in the form of a helix, and each leaflet is similarly coiled. Such a method of folding is spoken of as **circinnate,** from the Latin *circinnus*, a bishop's crozier (Fig. 471). The mature leaf only lasts one season and a crop of ten to twenty fresh leaves is produced each year, in a spiral succession continuous with those of previous years. The rudiments of next year's leaves form a close group over the stem apex.

The roots are of two kinds; firstly the single main root, which is produced by the embryo and dies away very early, and secondly roots which are termed **adventitious,** because they are produced secondarily from the tissues of the stem. Generally three such roots are produced at the base of each petiole. These roots are very slender and extensively branched, so that an old stem becomes almost completely covered by a mass of adventitious roots.

Anatomy of the Stem

In the simpler members of the Pteridophyta the stem consists of a single central **stele** surrounded by a **cortex,** but in many Ferns the structure becomes more complicated by the breaking up of this stele into a ring of steles which form a network. Each piece of this network is termed a **meristele,** and the whole structure is said to be **dictyostelic** (see p. 561).

Fig. 472 is a photograph of the stelar structure of a Fern stem from which all the parenchymatous tissue has been removed, leaving only the vascular skeleton. The meristeles form a tubular network with large diamond-shaped meshes, and each mesh corresponds to the base of a leaf. These are the **leaf gaps.** From the lower side of each mesh a number of slender meristeles emerge. These are the **leaf traces** which in the intact stem traverse the cortex and enter the petioles. Since the leaf bases of the Male Fern entirely cover the surface of the stem, any transverse section cut across the stem must necessarily be surrounded by the bases of leaves, whose traces are cut obliquely (Fig. 473).

Each meristele consists of a central core of **xylem** surrounded by **phloem.** The xylem is composed of **scalariform tracheids** and **xylem parenchyma.** The tracheids are large and polygonal in transverse section. There are no vessels in *Dryopteris*. Near the centre in small circular meristeles, or at the foci in larger elliptical ones, are one or two groups of much smaller tracheids which bear spiral or reticulate thickenings. These are the **protoxylem** elements, that is to say, the first xylem cells formed from the apical meristem. They differ, as usual, in their thickening from the mature xylem or **metaxylem.**

The phloem consists of a single ring of large **sieve tubes.** They are very long and tapering and the pointed ends overlap. Where two sieve tubes are in contact the walls bear numerous closely arranged **sieve plates,** which show minute adhering globules. There are no companion cells, but

FIG. 471.—*Dryopteris filix-mas.* Plants showing circinnate unfolding of leaves in spring of the second year.

there is a good deal of **phloem parenchyma,** which is continuous inwards with the xylem parenchyma. Together they are sometimes called the **conjunctive tissue.** Around the phloem lies a ring of squarish, thin-walled cells, the **pericycle,** which constitutes the outer limit of the meristele. Outside this is the **endodermis,** with Casparian bands on the radial walls of its cells. This is the innermost layer of the cortex. Outside it lies the massive cortical parenchyma.

Fig. 472.—*Dryopteris filix-mas.* Two dictyosteles dissected out from the stem showing wide leaf gaps and numerous leaf traces.

The arrangement of tissues in the meristele is therefore **concentric.** It is laid down once and for all from the primary apex and there is no provision for subsequent expansion. Each meristele is therefore a complete tissue system within its own endodermis. There is no common endodermis surrounding the dictyostele as a whole.

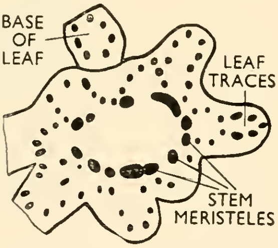

Fig. 473.—*Dryopteris filix-mas.* Diagram of transverse section of the stem showing arrangement of vascular tissue. (*After de Bary.*)

The rest of the cortex is made up of large parenchyma cells rich in starch, with walls of increasing thickness towards the periphery, while the outermost layers are almost completely sclerenchymatous. The **epidermis** is composed of cells with thick outer walls, and bears the chaffy scales or **ramenta.** These scales are made up of a plate of tissue one cell thick. They are apparently modified hairs and arise, like other hairs, from epidermal cells. They occur chiefly at the apex, which they entirely cover. The dark brown coloration, which is so common in all Fern stems and roots, is due to phenolic condensation products called phlobaphenes, chemically related to Bakelite, the well-known plastic material. A rare anatomical peculiarity found in the Male Fern is the occurrence in the cortex of many schizogenetic cavities lined with glandular hairs. These internal hairs secrete a resin which is a valuable vermifuge.

The stems of all Ferns grow from a single **apical cell,** which is usually shaped like a three-sided pyramid, with its base uppermost. This cell divides repeatedly, parallel to each of its three sides, and from it are derived all the cells of the mature tissues. In this the Ferns differ from the Spermatophyta, where, as we have previously seen, there is an apical meristem tissue, not a single apical cell.

ANATOMY OF THE LEAF

The leaves of the full-grown Male Fern are large, and consequently we find that five to seven leaf traces pass out from the stele into the petiole.

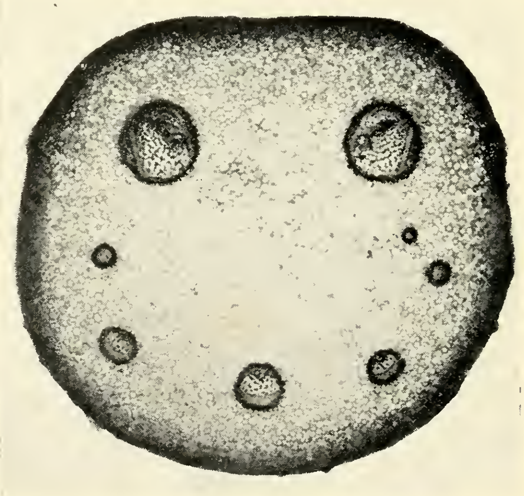

FIG. 474.—*Dryopteris filix-mas.* Transverse section through the petiole showing horseshoe arrangement of meristeles. From the two large adaxial meristeles the pinna traces are given off.

In transverse section the petiole is roughly semicircular in outline, the flattened side being **adaxial,** that is, towards the stem. The meristeles are arranged in the shape of a horseshoe with the points towards the adaxial side of the petiole, and are embedded in ground parenchyma, which is surrounded on the periphery by several layers of sclerenchyma (Fig. 474). In the upper part of the rachis the two marginal steles of the horseshoe give off branches to each pinna, and from these in turn branches are given off to the right and the left, which enter the pinnules and form the veins of their laminae.

The upper surface of the lamina is formed by an **epidermis,** beneath which is a **mesophyll,** composed of irregular parenchymatous cells with large intercellular spaces. Not only do the mesophyll cells contain chloroplasts but the epidermis does also. This is a character which the Ferns share only with shade-loving and with submerged aquatic Angiosperms. The presence of chloroplasts in the epidermis indicates that this layer differs markedly in its physiological importance from the epidermis of higher plants. In many Ferns the epidermis cells have lobed inner walls, simulating the arm-palisade of some Angiosperms, and the epidermis is not only strongly photosynthetic but is also the principal channel of translocation.

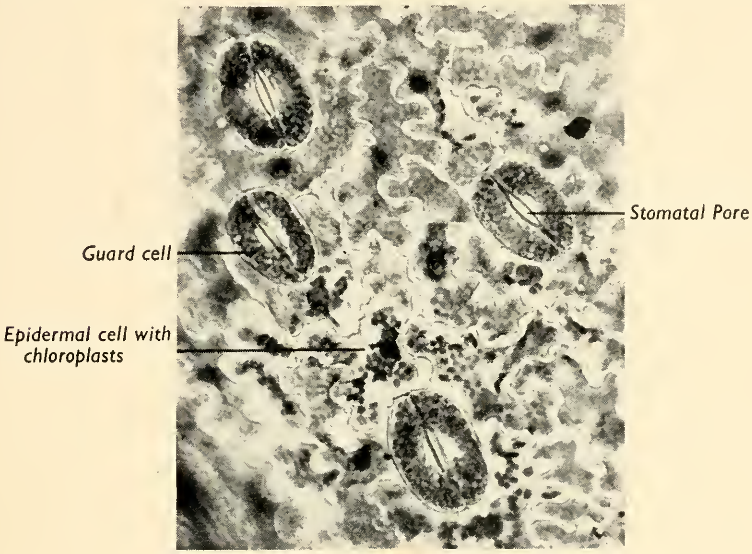

FIG. 475.—*Dryopteris filix-mas.* Lower epidermis of pinnule showing stomata and irregularly shaped epidermal cells containing chloroplasts.

Below the mesophyll lies the lower epidermis, in which are the **stomata** (Fig. 475). These stomata consist of a pair of specialized curved cells, which are termed the **guard cells,** and these surround a narrow slit, which is referred to as the **stomatal pore.** By variation in the shape of the guard cells this pore may be opened or closed, and it is by this means that the interchange of gases between the atmosphere and the leaf is regulated. We shall consider later (Volume III) the mechanism of the opening and closing of stomata. In common with the other organs, the Fern leaf also grows from an apical cell, in this case two-sided, from which two marginal series of cells are derived, which in turn produce the cells of the lamina. The growth of the young leaf is thus marginal as well as apical.

Anatomy of the Root

The adventitious roots arise at the bases of the leaves, though their steles are in direct communication with the stele of the stem. The development of these roots begins in specialized cells of the endodermis of the stem stele.

In structure the root is relatively simple (Fig. 476). In the centre is a small **xylem** with two **protoxylem** groups, one at each end. A stele like this, in which there are two protoxylem groups, is said to be **diarch.** The xylem plate between the protoxylems has a constant orientation parallel to the axis on which the root is borne. Outside the xylem lie two groups of **phloem** elements arranged laterally to the xylem plate. There is also a limited parenchymatous conjunctive tissue. Surrounding the phloem is a double-layered **pericyle,** followed by a single-layered **endodermis.** The **cortex** consists of a very thick-walled inner zone and a thin-walled outer zone, so that it appears double. Like the stem, the root has a single large, pyramidal, **apical cell** with three sides, from which all cells of the organ, with the exception of the root cap, are cut off by successive divisions. The cells of the root cap are cut off from the base of the apical cell. Each cycle of three divisions parallel to the sides of the pyramid is followed by one parallel to the base, so that every fourth cell formed is added to the tissue of the root cap.

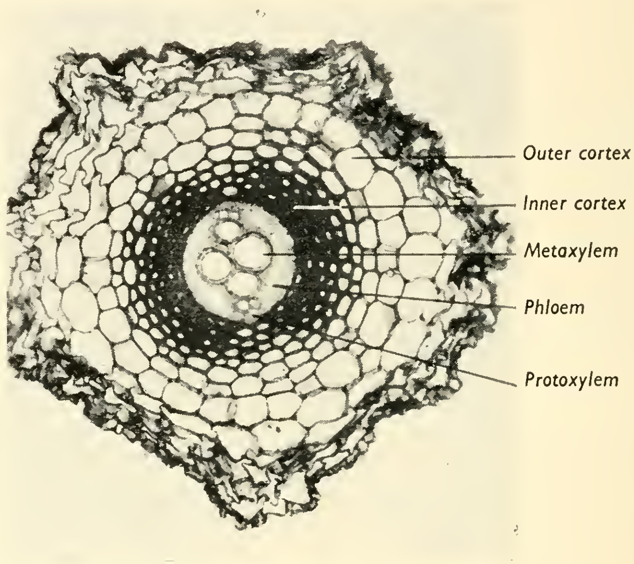

Fig. 476.—*Dryopteris filix-mas.* Transverse section of root.

Development of the Sporangium

The spores are produced on certain leaves of the mature plant which may therefore be called **sporophylls.** In *Dryopteris* the vegetative leaves and sporophylls are alike, but the sporophylls only occur on older plants. The **sporangia** are arranged in small kidney-shaped groups called **sori,** which are produced in two rows on the under surface of each pinnule of the leaf (Fig. 477). The sporangia are attached to a cushion-like swelling, the **placenta,** from which also arises a delicate membrane, the **indusium,** which covers the sorus like a hood (Figs. 478 and 479). The sorus is at first pale green, but becomes chestnut brown as the sporangia ripen. A single vein of the leaf ends in each placenta and supplies it with nutriment. Sporangia develop successively but without any regular order.

Fig. 477.—*Dryopteris filix-mas.* Lower surface of a portion of a fertile pinna showing sporangial sori, still partially covered by the indusia, arranged in two rows on the pinnules.

The sporangium originates from a single superficial cell of the placenta (Fig. 480). This cell divides into two, and the upper cell divides again by a wall at an oblique angle to the first wall. By a further oblique division, a tetrahedral cell is formed, the upper part of which is cut off again by a transverse wall. The inner cell thus formed is the **archesporial cell** (Fig. 481). Meanwhile, the lower cell of the pair formed at the first division has divided up to form a multicellular tissue, the **stalk.** The cells surrounding the archesporial cell divide further, and give rise to the wall of the sporangium.

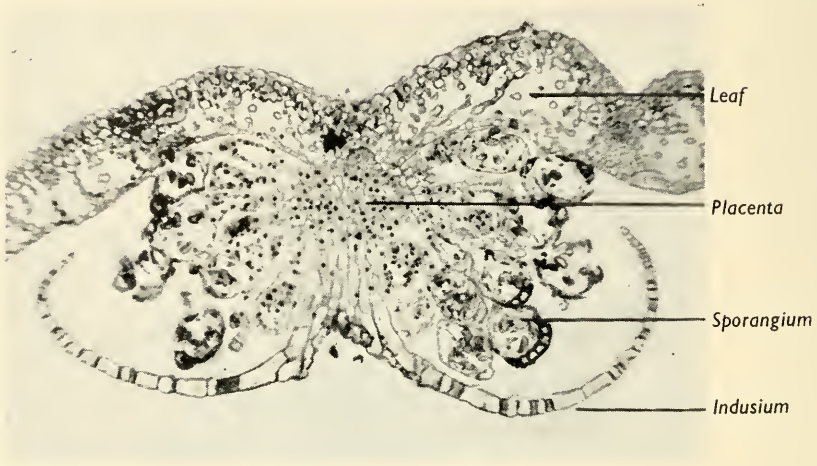

FIG. 478.—*Dryopteris-filix mas.* Transverse section of pinnule through a sorus showing developing sporangia.

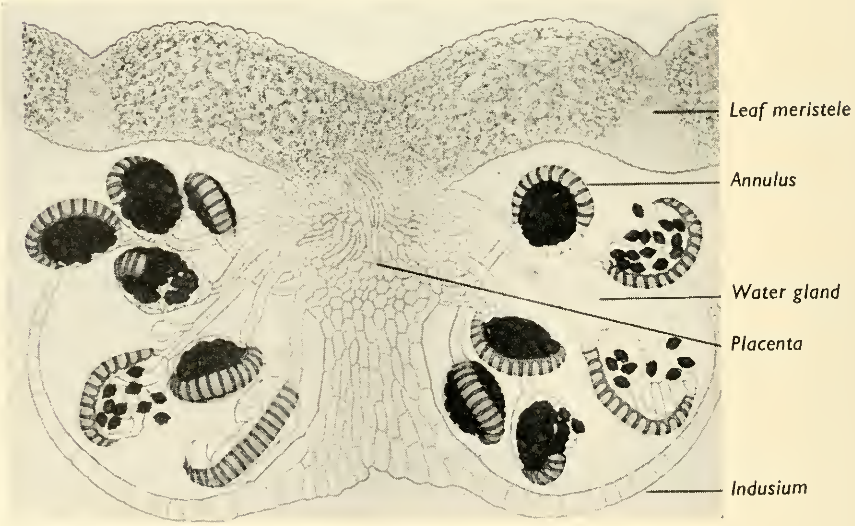

FIG. 479.—*Dryopteris filix-mas.* Transverse section of pinnule through a sorus showing mature sporangia, some of which are dehiscing. (*From Kny.*)

The archesporial cell then divides to produce a transitory layer of cells on the outside, termed the **tapetum,** and a small number of central cells, usually about twelve in number, called the **spore mother cells.** It is from these mother cells that the spores are developed. Each spore mother cell divides into four **spores.** During the divisions of each spore mother cell there is a **meiosis,** in which the chromosome number is halved. We see, therefore, that in each mature sporangium there are forty-eight spores, and each spore contains the monoploid number of chromosomes.

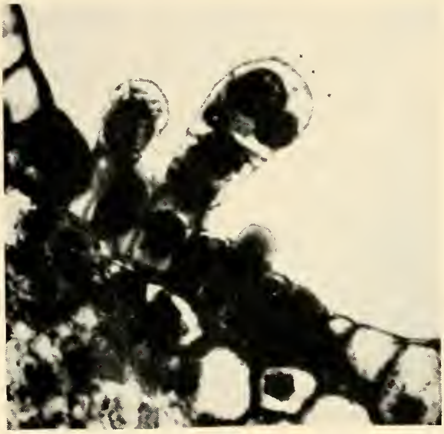

FIG. 480.—*Dryopteris filix-mas.* Rudiments of sporangia showing their origin from single epidermal cells.

The **sporangium** itself is a small, stalked capsule containing the spores which have dark, rugged walls. The capsule is not spherical, but is shaped like a biconvex lens. The wall of the sporangium is composed of a single layer of cells, which are flat and thin-walled, except round the edge, where a row of specially thickened cells, called the **annulus,** partially surrounds the capsule. Where it stops short on one side, there is a group of narrow thin-walled cells, the **stomium,** at which point the ripe sporangium breaks open.

The bursting of the sporangium is caused by a very effective mechanism. As will be seen from Fig. 482, the cells of the annulus are peculiarly thickened; the inner tangential and radial walls are thick, while the outer tangential wall is thin. It is due to the behaviour of the cells of the annulus in relation to water that the bursting of the sporangium is achieved. In a young state water glands are developed on the stalks of the sporangia, which secrete moisture and maintain a damp atmosphere under the indusium. When the sporangia are mature the indusium shrivels and the glands cease to secrete. The sporangia thus become exposed to dry air and loss of water from the cells, due to evaporation, causes the thin outer walls of the annulus to contract. Meanwhile the water which is held in cohesion between the thickened radial walls tends to draw them together. Under the strain so produced the cells of the stomium are torn asunder and the annulus, together with part of the sporangium wall, springs back, throwing out the spores. As evaporation continues a point is reached where the cohesion of the water in the cells of the annulus breaks down and air enters the cells. This allows the cells of the annulus to expand again and the sporangium wall snaps back into its original position, thus scattering any spores which still remain in the sporangium.

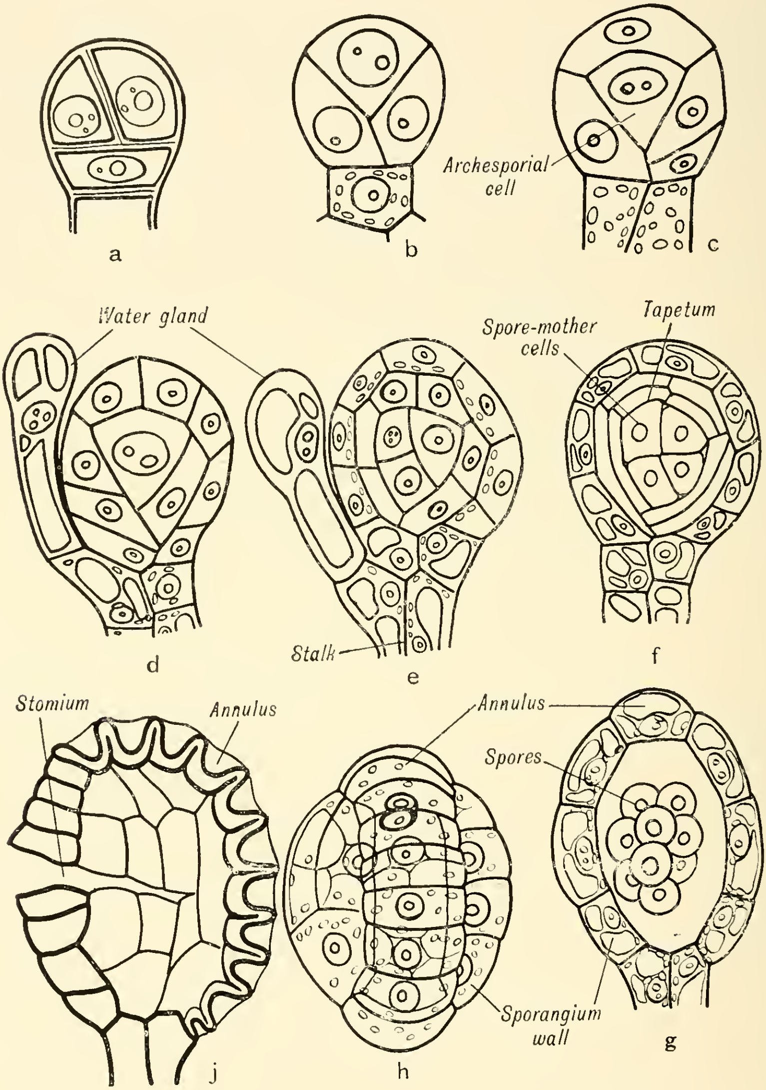

FIG. 481.—*Dryopteris filix-mas.* Stages in the development of a sporangium. (*After Kny.*)

The output of spores from a mature *Dryopteris* plant is of the order of five hundred million in a single season. Only a minute percentage of these ever develop into new plants, but they may remain dormant in the soil for a long time, and owing to their numbers they must be almost ubiquitously distributed.

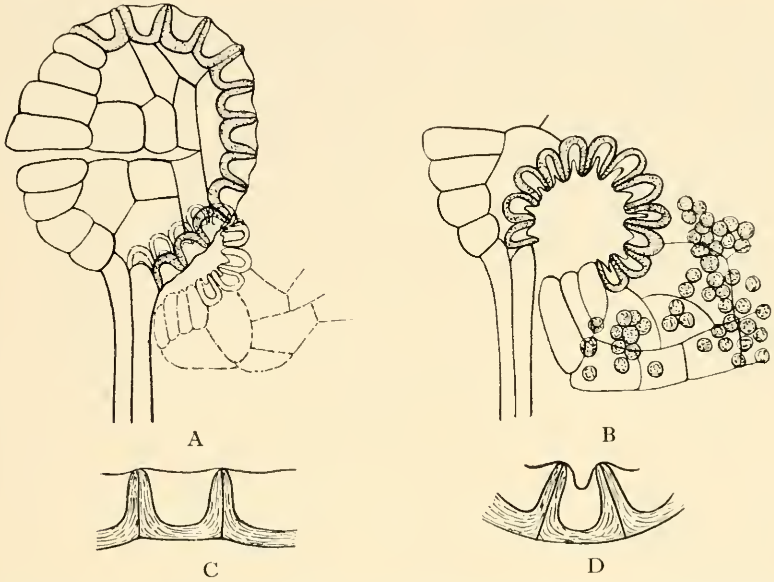

FIG. 482.—*Dryopteris filix-mas.* Dehiscence of sporangium. A, Sporangial wall splitting through stomium. B, Annulus retracted and spores being discharged. C, Cells of the annulus before retraction. D, Contracted annulus after dehiscence. (*After Bower.*)

DEVELOPMENT OF THE PROTHALLUS

The spores lie dormant in the ground for some time, and at length germinate. The spore wall breaks and a green cell emerges, from which a colourless branch grows into the soil and forms a **rhizoid.** The green cell then divides and a filament is formed (Fig. 483) which grows by means of an **apical cell,** that is, a terminal cell which at first only cuts off cells behind it. By subsequent lateral divisions of the apical cell the flat **prothallus** or **prothallium** is formed (Fig. 484). The prothallus is usually heart-shaped, but this depends to a large extent upon its environment. When a number of prothalli are crowded together they never reach the heart shape but remain more or less filamentous and minute. In a well-developed prothallus only the central part is more than one cell thick: this part is called the **cushion,** and on its under surface **rhizoids** develop, attaching the prothallus to the soil. The formation of the cushion is associated with a stage in development at which the original apical cell is replaced by a group of initial cells. During the growth of the prothallus the cells cut off from the apical cell expand rapidly, thus leaving the actual apex at the bottom of an indentation and producing the characteristic heart shape.

The prothallus is a self-supporting organism whose cells contain numerous chloroplasts and are able to perform photosynthesis, and whose rhizoids can obtain mineral matter from the soil. The prothallus represents the **gametophyte generation** of the Fern, so called because the sex organs are developed at this stage.

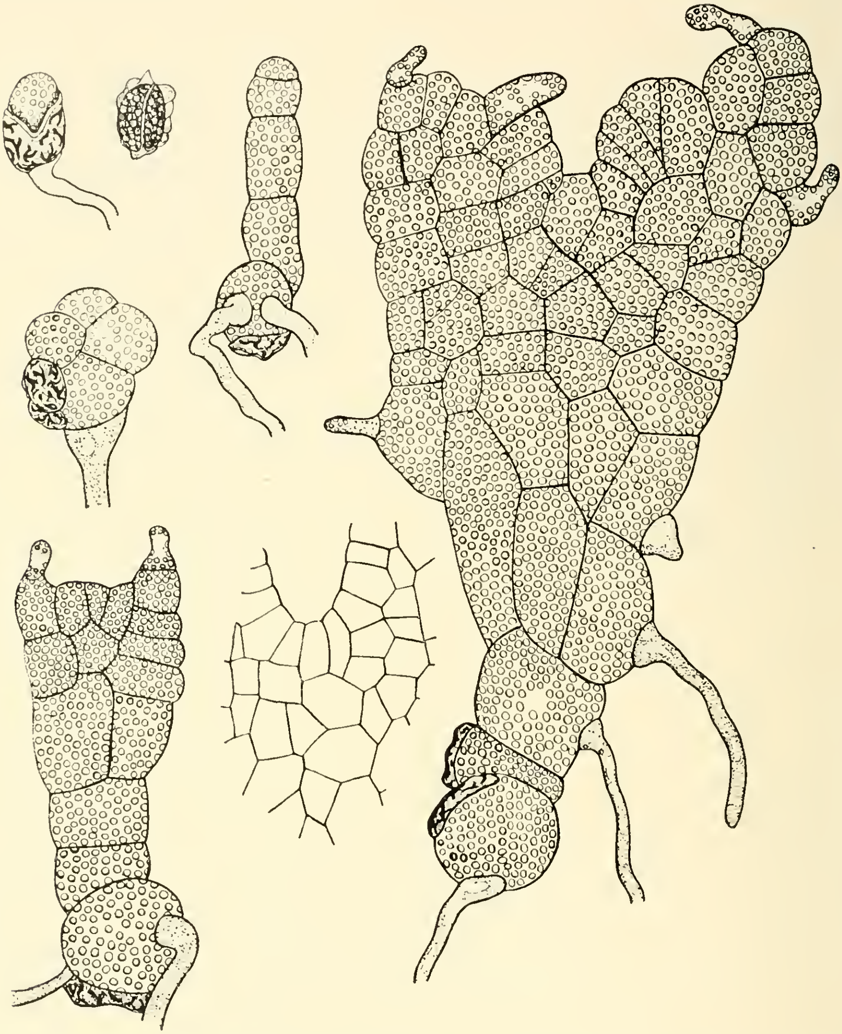

FIG. 483.—*Dryopteris filix-mas.* Germination of the spore and early stages in the development of the prothallus showing differentiation of the apical cell and beginnings of lateral expansion. (*After Kny.*)

Hidden on the inconspicuous prothallus the sex organs of the Fern were for long unknown. This gave rise to the term **cryptogam** (or " hidden marriage "), which was applied generally to all the flowerless plants. The sexual reproduction of the Fern was discovered by Suminski in 1848, and it has subsequently been elucidated in nearly every group, so that the name Cryptogam is now an obsolete survival.

The mystery surrounding the reproduction of Ferns was realized even in early times, and " fern-seed " figures along with other equally unobtainable commodities in many magical formulae of the Middle Ages.

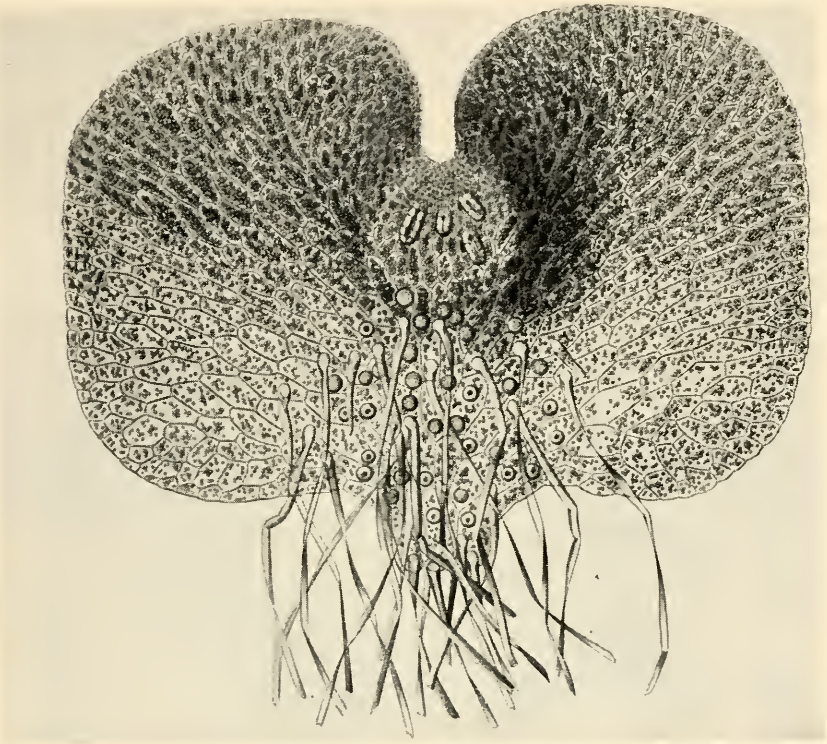

FIG. 484.—*Dryopteris filix-mas.* Mature prothallus seen from below showing rhizoids, among which are antheridia and, above, archegonia arising on the cushion behind the growing point. (*After Suminski*, who first discovered Alternation of Generations in Ferns.)

DEVELOPMENT OF THE SEX ORGANS

The male sex organs, or **antheridia,** appear while the prothallus is still quite small, and in poorly developed specimens they may be the only ones formed, that is to say, the prothallus is unisexual. But in well-grown prothalli the female organs, or **archegonia,** develop later on the under side of the central cushion. Both are multicellular structures in which the gametes are enclosed and protected until they are mature. The archegonia are developed behind the notch in which lies the apex of the prothallus, while the antheridia are found farther back among the rhizoids, *i.e.*, near the posterior end of the prothallus. As the antheridia mature before the archegonia, we may assume that cross-fertilization between different prothalli is the general rule.

The antheridium develops from a single superficial cell of the prothallus (Fig. 485). By successive oblique divisions a central cell is isolated, surrounded by a number of peripheral cells which contain the chloroplasts of the original cell. The first division wall is funnel-shaped, with the wide end upwards. This is followed by a dome-shaped wall across the top of the funnel, thus enclosing a central cell. The upper cell then divides by a ring-shaped wall.

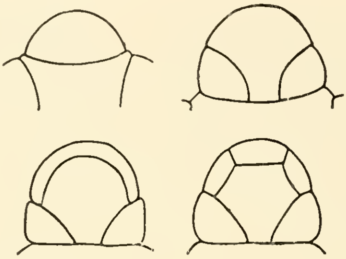

Fig. 485.—*Dryopteris filix-mas.* Diagram showing the succession of cell divisions in the formation of an antheridium. (*After Strasburger.*)

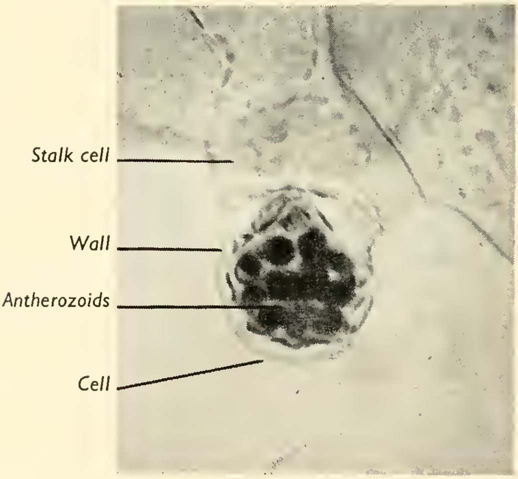

Fig. 486.—*Dryopteris filix-mas.* Mature antheridium on the surface of the prothallus.

The antheridium thus consists of two ring cells, one above the other, a discoid cap cell and the central cell.

The divisions of the central cell are irregular in number, but about thirty-two cells are usually formed, called **antherozoid mother cells,** and from these the **antherozoids** are developed (Fig. 486). Each nucleus is transformed into a tapering spiral of three turns, with a vesicle of cytoplasm at the posterior end. A dense band, called the **blepharoplast,** attached to the edge of the spiral at the thin end, bears a group of very long **flagella,** by means of which the antherozoid can swim actively in the water film between the prothallus and the soil. When the antherozoids are mature the walls of the mother cells become mucilaginous and swell, forcing off the lid cell of the antheridium. The antherozoids are ejected, each still contained in a cell wall, but this quickly dissolves and liberates the male gamete, which soon sheds all its adherent cytoplasm (Fig. 487).

Fig. 487.—*Dryopteris filix-mas.* Mature antherozoid with protoplasmic vesicle and flagella. (*After Yamanouchi.*)

The archegonium is an elongated organ, consisting of a **venter,** which is buried in the tissues of the prothallus, and a curved **neck,** which projects freely above it. The archegonium originates by the division of a superficial cell into two (Fig. 488). The lower of these is the **basal cell,** which contributes only to the building of the wall round the venter. The upper cell again divides transversely. Of the two cells formed from it, the upper one produces the four rows of cells that form the neck. Since the neck is curved,

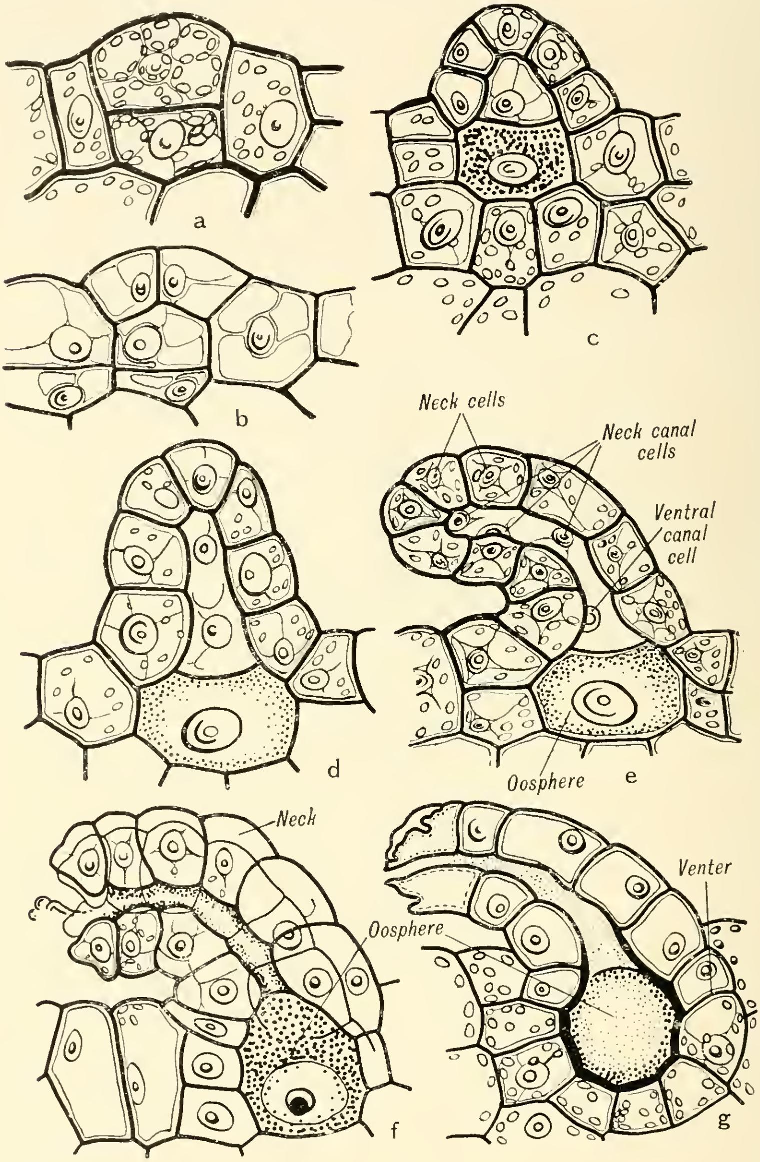

FIG. 488.—*Dryopteris filix-mas.* Stages in the development of the archegonium from a superficial cell of the prothallial cushion. (*After Kny.*)

the two rows on the convex side usually contain five to six cells, while those on the concave side have only four. The lower or central cell grows up between the neck cells and cuts off a narrow cell which is the **neck canal**

cell. This may again divide several times so that the axis of the neck is occupied by a file of cells with thin walls. The lower portion of the central cell divides into a small upper portion, the **ventral canal cell**, and a much larger portion which becomes the **oosphere** (Fig. 489).

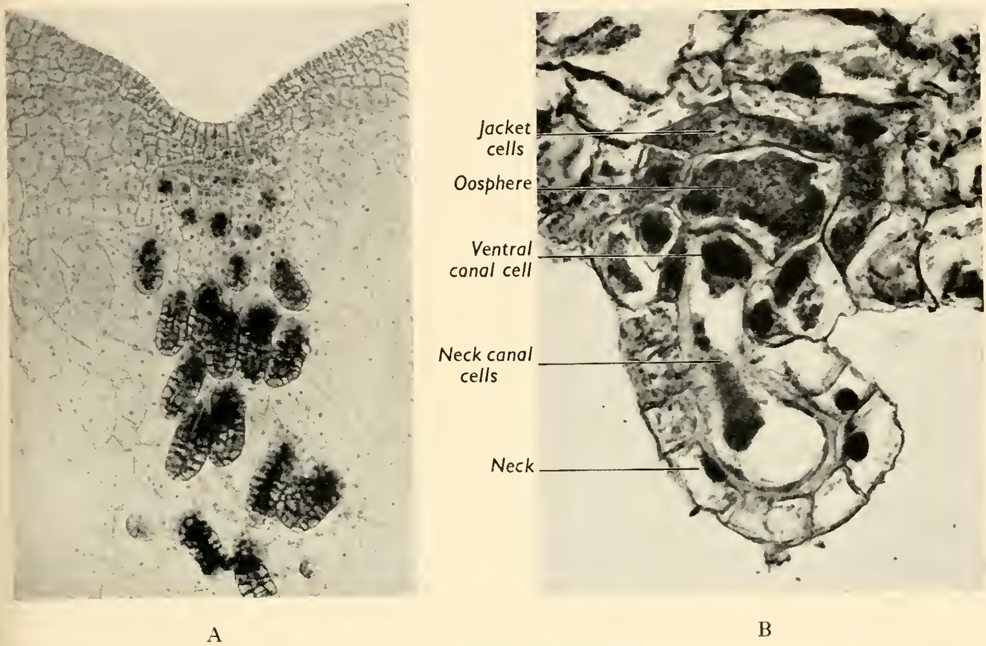

FIG. 489.—*Dryopteris filix-mas.* A, Archegonia developing on the lower surface of the prothallus behind the apical cell. B, Longitudinal section of mature archegonium before opening of the neck. Compare with Fig. 488, E.

(A, *By courtesy of the General Biological Supply House Inc., Chicago, Illinois.*)

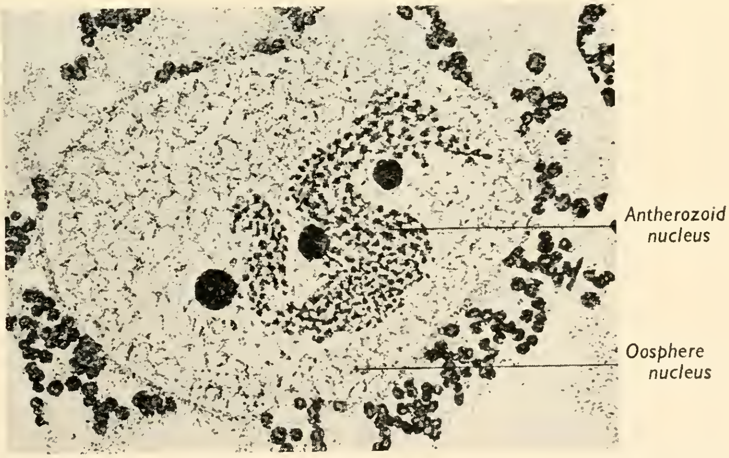

FIG. 490.—*Dryopteris sp.* Nucleus of oosphere after fertilization showing enclosed antherozoid nucleus. (*After Yamanouchi*).

The neck canal cells and the ventral canal cell break down into a mucilaginous material which swells and is extruded at the apex of the neck, forcing apart the neck cells and thus opening a passage down to the oosphere.

Fertilization and Development of the Embryo

The archegonium, when mature, secretes a substance, probably malic acid, which attracts to it by chemotaxis the actively swimming antherozoids. They make their way down the canal through the mucilage, and one enters the **oosphere** (Fig. 490) at a clear **receptive spot.** Fertilization occurs at

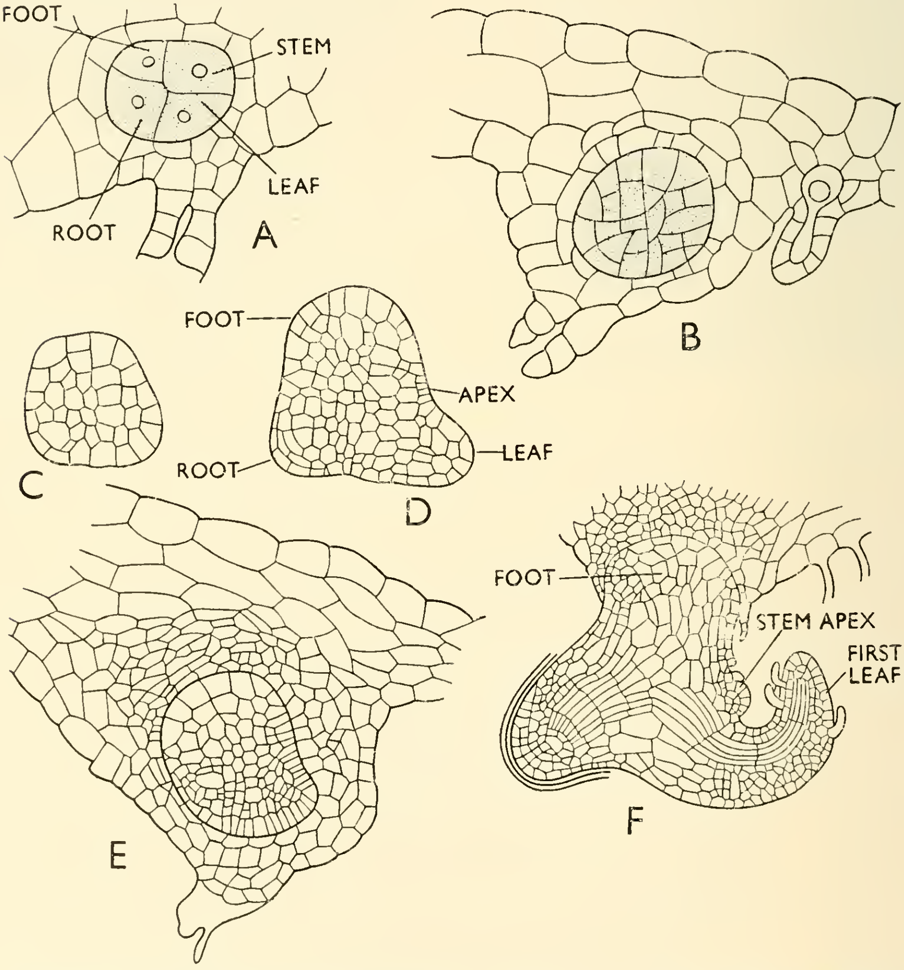

Fig. 491.—*Dryopteris filix-mas.* Development of the embryo. A, Four primary segments. B, Periclinal divisions establishing growing points of root, stem and leaf. C and D, Progress of differentiation. E, Embryo embedded in enlarged venter of archegonium. F, Embryo emerging from prothallus, primary root turning downwards, primary leaf turning upwards, foot still embedded in prothallus tissue. (*After Hofmeister.*)

once, the male and female fuse, and the oosphere secretes a wall, becoming an **oospore.** Although several archegonia may be fertilized, only one oospore in each prothallus finally comes to maturity.

Soon after fertilization the oospore divides vertically into two, and by a second and third division forms an octant or group of eight cells. Four of these, directed towards the apex of the parent prothallus, form the epibasal, and the other four the hypobasal hemispheres (Fig. 491). The former produces the axis and the first leaf of the embryo plant, the latter produces the primary root and a suctorial portion called the **foot,** which remains embedded in the archegonial venter (Fig. 492), and by which nourishment is obtained until the young plant becomes self-supporting. A small, diarch primary root is formed, but soon dies and is replaced by adventitious roots. When the first leaf has grown large enough to nourish the young plant, the prothallus usually disappears (Fig. 493). The first leaf is usually small and two-lobed. The immediately subsequent leaves become larger but are also

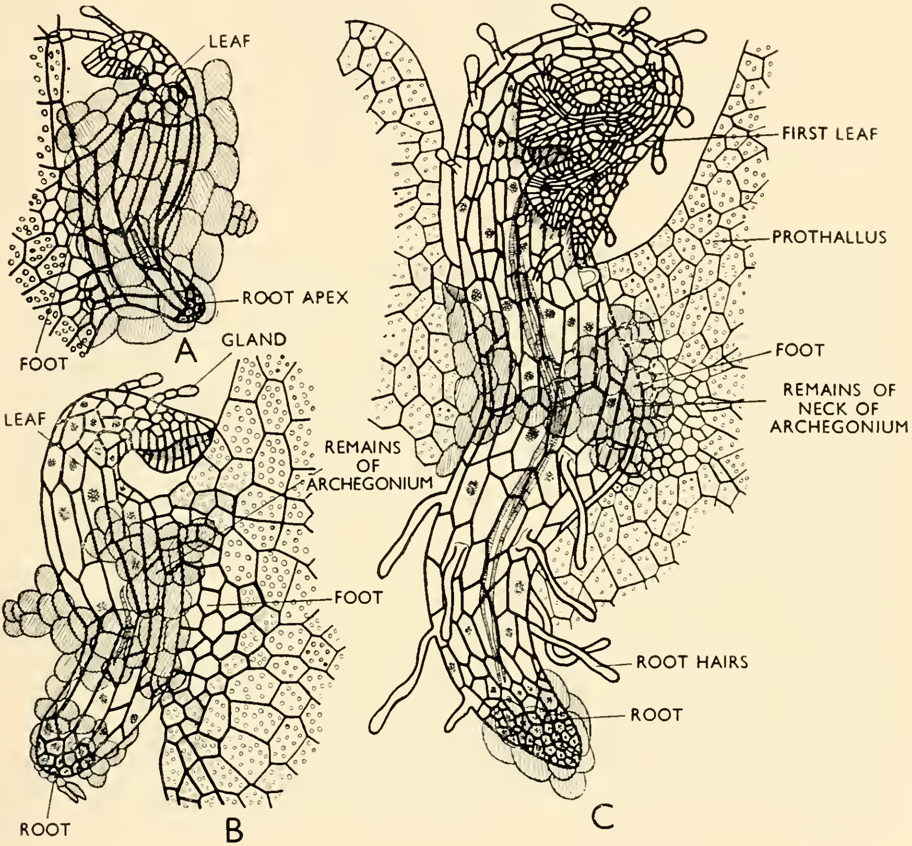

FIG. 492.—*Dryopteris filix-mas.* Stages in development of the embryo after emergence from the archegonium. (*After Suminski.*)

dichotomously divided. It is not until the fifth or sixth leaf is reached that the pinnate form of the mature leaf appears. This young sporeling develops into the ordinary Fern, and since it will later produce spores, it is spoken of as the **sporophyte generation.**

FIG. 493.—*Dryopteris filix-mas.* Prothalli with attached embryos illustrating the change from the palmate form of the earliest leaves to the pinnate form of the mature leaves.

ALTERNATION OF GENERATIONS

Since in the act of fertilization the chromosome number is doubled, the Fern plant to which it gives rise will have nuclei containing the double or diploid number of chromosomes. In the Fern the meiosis or halving of the chromosome number takes place in the formation of the spores. Thus the nuclei of all the cells of the prothallus and the sex organs and gametes borne on it will have the single or monoploid number. It may be said, therefore, that the Fern exhibits an alternation of monoploid and diploid generations.

The diploid generation is called the **sporophyte,** while the monoploid part of the life-cycle is called the **gametophyte.** Thus the alternation of two morphologically different generations corresponds to two cytologically different phases (FIG. 494).

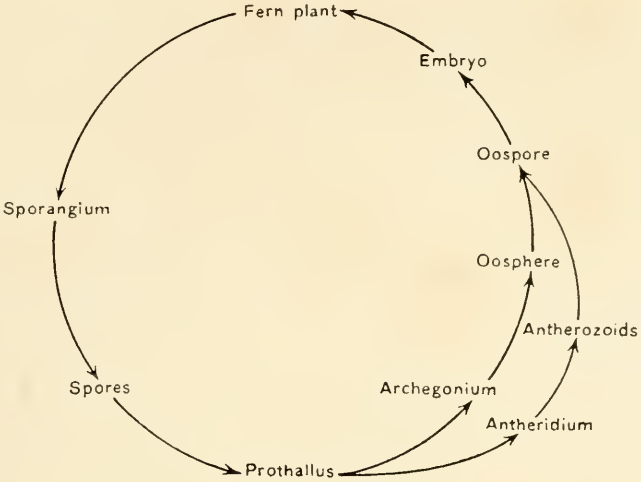

FIG. 494.—Life-cycle of *Dryopteris filix-mas.*

Pteridium aquilinum (The Bracken Fern)

The common Bracken Fern, *Pteridium aquilinum,* occurs very commonly in this country on open heath land and in sandy woods (Fig. 495). In its life-history, and to some extent in its structure, it resembles the Male Fern, but there are certain important differences.

The plant consists of a creeping underground stem or **rhizome,** from which are given off vertically growing leaves. Each leaf consists of a very long stem-like petiole and a large, compound lamina, which is triangular in outline. Pinnae are few and are stalked ; each bears stalked pinnules, and these are again subdivided. We realise, therefore, that the only part of the Bracken Fern which we normally see above ground is the leaves, and the structure which is frequently erroneously regarded as the stem is really the petiole of the leaf.

The true stem is the blackish-coloured rhizome, which grows very vigorously underground and is the plant's chief means of spreading. It grows by means of a single wedge-shaped, *i.e.* two-sided, **apical cell** (Fig. 496), and branches **dichotomously,** that is, by division of the apical cell, into two equal parts. The two limbs do not, however, develop equally (Fig. 497). One branch usually remains very short for some time and bears a leaf so close to its base that the apex looks like an adventitious bud on the base of the leaf petiole.

This leaf is, in fact, an **angular leaf,** that is to say, it originates at the point of dichotomy of the stem, a feature which is not uncommon in the Filicales. It is secondarily shifted on to the weaker limb of the dichotomy, on which it appears to arise, but its vascular system is connected directly to that of the main stem. This is the reverse of the condition found in *Dryopteris*, where the lateral buds are attached to the leaf petioles.

Fig. 495.—*Pteridium aquilinum* growing in a wood. Much reduced.
(From Step, " Trees and Flowers of the Countryside," Hutchinson & Co. Ltd.)

The rhizome has definite upper and lower sides, that is, it is **dorsiventral.** It bears leaves alternately to right and left as well as adventitious roots.

The leaves are very slow to mature. During the first year only an inch or so of the petiole develops and there is no lamina (Fig. 498). During the second year a minute lamina forms, folded over the apex of the petiole, but it is not till the third season that the petiole comes above ground and the lamina expands to its full size. Both stem, apex and young leaf are thickly set with brown ramenta, but the leaf sheds them as it grows.

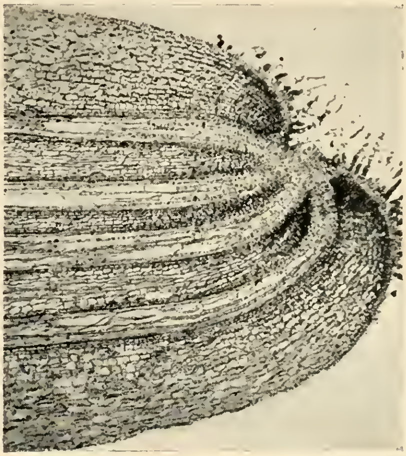

Fig. 496.—*Pteridium aquilinum.* Longitudinal section through the apex of the rhizome showing the apical cell and differentiation of meristeles. (*After Chang.*)

At the bases of the first two leaf pinnae there are **nectaries,** little sunken patches of tissue from which a sugary secretion escapes, through the stomata. Their function is unknown.

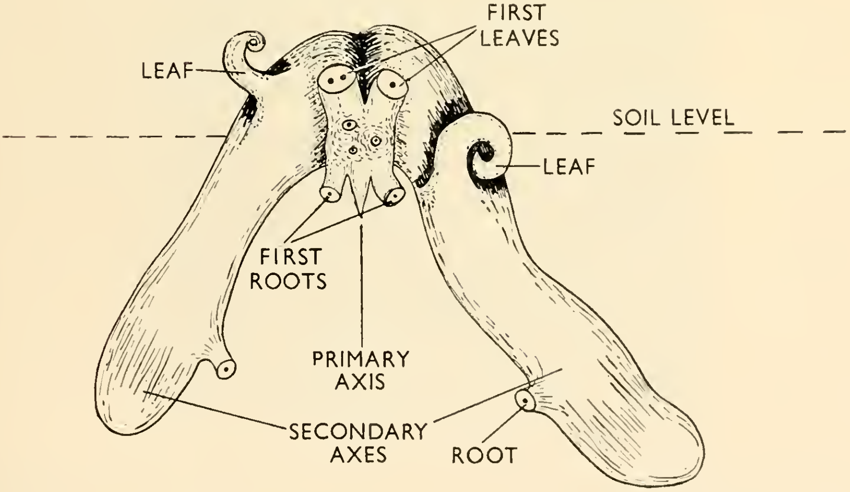

Fig. 497.—*Pteridium aquilinum.* Primary dichotomy of the rhizome. (*After Bower.*)

The points on the rhizome at which the leaves are given off are termed the **nodes,** whilst the spaces between the nodes are called **internodes.** In the Male Fern the leaves are set so closely together in succession that there are no internodes on the stem. In the Bracken the internodes are long, and on this account it is easier to study the anatomy of the stem of the Bracken than that of the Male Fern.

FIG. 498.—*Pteridium aquilinum.* Apex of rhizome with three successive stages in the development of leaves.

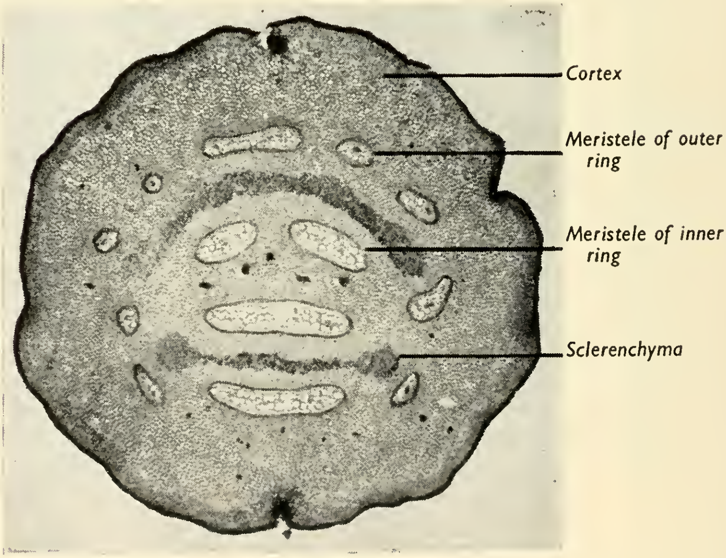

FIG. 499.—*Pteridium aquilinum.* Transverse section of the rhizome showing two concentric rings of meristeles separated by two arcs of sclerenchyma.

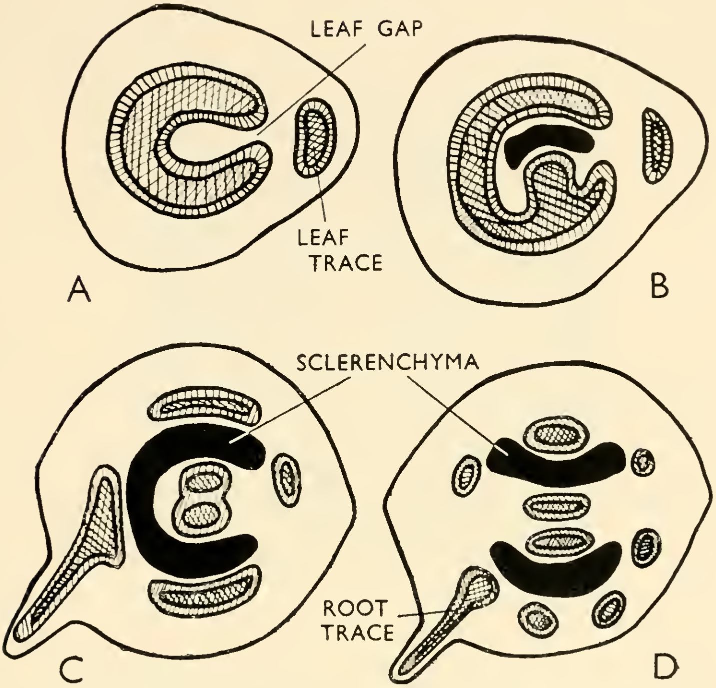

Fig. 500.—*Pteridium aquilinum.* Diagrams of successive stages in ontogeny of the rhizome. A, Solenostelic condition with single leaf gap. B, Origin of the internal stele as a branch from the external stele. C, Dictyostelic condition established in outer stele. D, Dictyostelic condition in both steles. (*After Jeffrey.*)

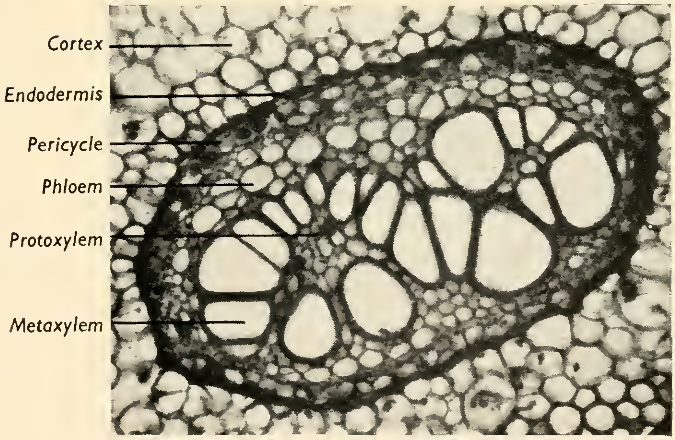

Fig. 501.—*Pteridium aquilinum.* Transverse section of meristele in the rhizome showing two protoxylem groups.

ANATOMY OF THE STEM

The stem consists of an outer limiting zone of brown sclerenchymatous cells, inside which is a cortex of thin-walled parenchyma filled with starch.

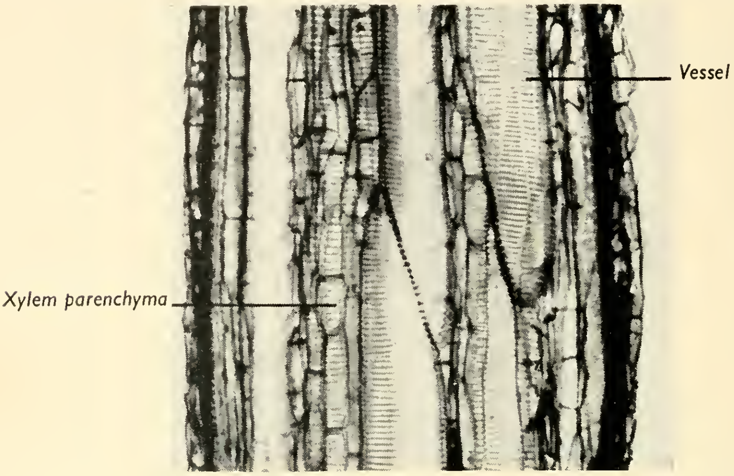

FIG. 502.—*Pteridium aquilinum.* Longitudinal section of meristele showing perforated end wall of vessel.

There are two concentric steles present, each having the form of a tubular network of meristeles (Fig. 499). Unlike the meristele of *Dryopteris*, the meshes of the network all correspond to the insertions of leaves, that is, they are **leaf gaps.** In *Pteridium* there are also leaf gaps, but as the leaves are far apart there are numerous additional gaps, not related to the leaves, which are called **perforations.** Between the two concentric steles there lie two thick bands of sclerenchyma, the dorsal band arched and the ventral (*i.e.*, the lower) one more or less flat. Sometimes their edges unite to form a tube, like the steles.

The two steles are independent of each other, except at the nodes, where **leaf traces** originate from both inner and outer steles and accessory branches may link them together. The condition found in *Pteridium* is called **polycycly** and is not uncommon in thick Fern stems. It is no doubt useful in improving the vascular supply to a massive tissue system (Fig. 500).

FIG. 503.—*Pteridium aquilinum.* Longitudinal section of sieve tube showing numerous lateral sieve areas.

The structure of the individual meristeles is very similar to that in the Male Fern (Fig. 501), but there is an important peculiarity in that the end walls of the large scalariform elements are perforated, so that they form true **vessels,** which are of rare occurrence in Cryptogams (Fig. 502).

The sieve tubes are of a primitive type, their lateral walls being covered with sieve areas (Fig. 503). It has been found that the parenchyma cells in the phloem are sister cells of the sieve tubes, so that, in character if not in form, they represent companion cells. The phloem cells are all derived from the same cells as those which produce the pericycle and endodermis, and the latter tissue is therefore in this case part of the stele instead of being, as is usual, the innermost layer of the cortex.

Structure of the Petiole

The petiole shows, in section, a large number of meristeles, arranged apparently at haphazard. In small petioles, however, with a smaller number of meristeles, it is possible to see that their arrangement is that of a much-convoluted horseshoe, with the open side adaxial, that is, towards the upper side of the petiole. The significance of this arrangement is explained later (p. 561). An irregularly T-shaped band of sclerenchyma lies inside the horseshoe. The meristeles at the two ends of the horseshoe are derived from the inner of the two steles of the rhizome (Fig. 504).

Fig. 504.—*Pteridium aquilinum.* Transverse section of a young petiole before the formation of sclerenchyma.

Structure of the Root

The roots arise adventitiously from the rhizome and are blackish and wiry in texture. Their anatomy essentially resembles that of the *Dryopteris* root, but there are two unusually large metaxylem vessels standing side by side in the middle of the xylem plate. They project sideways into the phloem zone and separate the two phloems into four, giving a superficial resemblance to a tetrarch instead of a diarch structure (Fig. 505).

There is a remarkable anatomical similarity among all Fern roots, even in fossil Ferns from the Carboniferous, however widely the stem structures may differ. This is sometimes expressed by the saying that the root is a " conservative organ."

The Sporangium

The sporangia of the Bracken Fern form a continuous line close beneath the margin of the leaf instead of being distributed in separate sori (Fig. 506). The placenta actually originates from the leaf margin itself, but it is concealed by an indusium which is folded over it and gives the appearance of being an infolded leaf margin. A second indusium is also formed on the inner side of the placenta, so that the sporangia are enclosed between them, a peculiarity of this Fern. Both these indusia are outgrowths from the leaf surface.

The development of the sporangia is essentially similar to that in the Male Fern. They arise without any regular succession on the placenta, and each possesses an annulus and stomium similar to that of *Dryopteris* (Fig. 507). Within the sporangium numerous spores become differentiated (Fig. 508), which are liberated by the bursting of the sporangium at the stomium under the influence of the contracting annulus.

The Gametophyte

The spores on being shed germinate to produce a prothallus, which is similar in appearance to that of *Dryopteris*. On this prothallus, antheridia and archegonia develop which give rise respectively to antherozoids and an oosphere, and as a result of the conjugation of these gametes an embryo is formed which develops into a fresh Bracken plant. In all these stages there is no important distinction between *Dryopteris* and *Pteridium*, and it will not, therefore, be necessary for us to consider them in detail.

Leptosporangiatae : Hymenophyllaceae

The Hymenophyllaceae or " Filmy Ferns " are a small group of Ferns with very delicate leaves which grow in very damp and shady places, usually in forests. In tropical rain forests many species are epiphytic.

The slender, protostelic stems are creeping, and usually have adventitious roots, though in some forms the rhizome-branches function as roots and are provided with root hairs. The leaves are borne in two rows and the lamina is only one cell thick and translucent. The sori are marginal, the placenta being formed by the prolongation of the end of a vein beyond the edge of the leaf. The sorus is enclosed by a cup-like indusium, which may be two-lipped or divided into two valves. The sporangia are sessile, with an oblique annulus, and develop in basipetal succession on the placenta (*Gradatae* of Bower). The prothallus is filamentous or strap-shaped.

There are only two genera in the family: *Hymenophyllum* with a two-lobed indusium and *Trichomanes* with an indusium in one piece. We shall deal in detail only with the former genus.

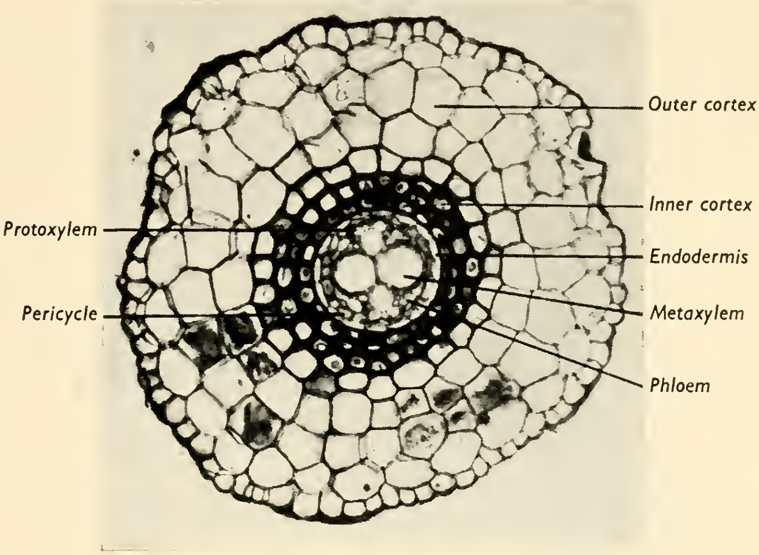

FIG. 505.—*Pteridium aquilinum.* Transverse section of the root.

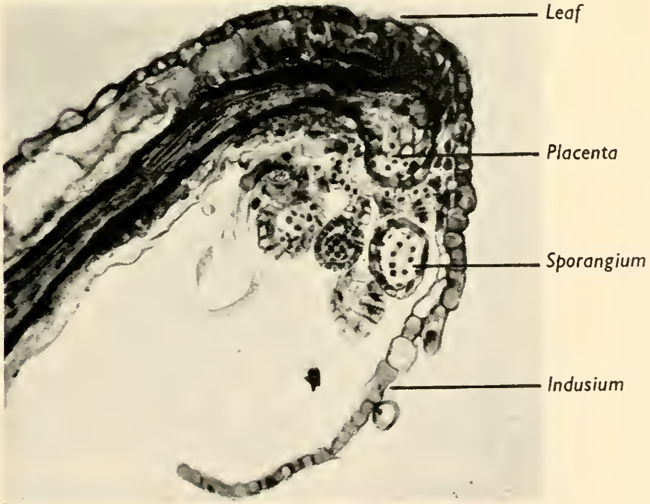

FIG. 506.—*Pteris serrulata.* Transverse section through marginal sorus showing developing sporangia. In the genus *Pteris* no second indusium is present.

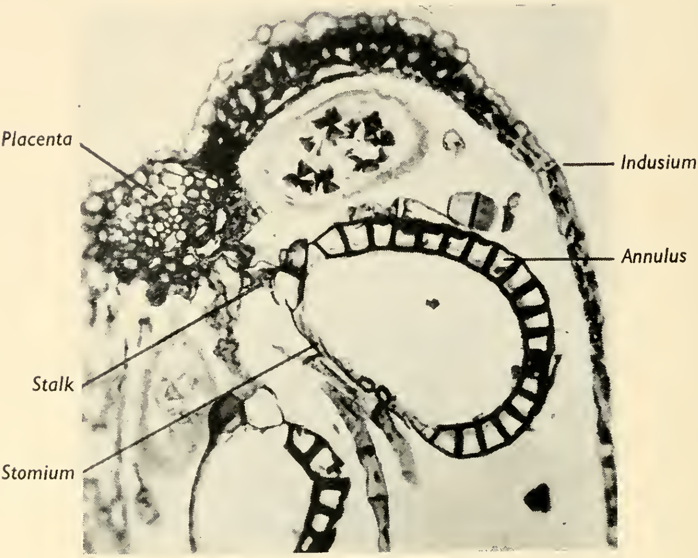

FIG. 507.—*Pteris serrulata.* Section through marginal sorus with mature sporangia.

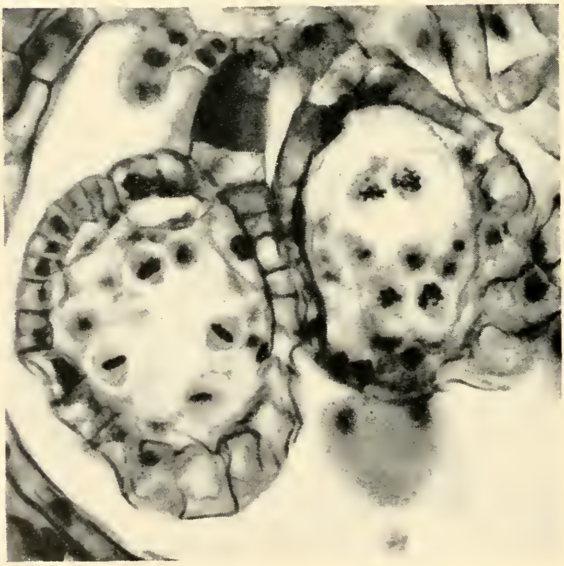

FIG. 508.—*Pteris serrulata.* Metaphase stages of meiosis in spore mother cells.

Hymenophyllum tunbridgense

The genus *Hymenophyllum* has about 300 species, mostly tropical, although two, *H. tunbridgense* and *H. unilaterale* (*wilsoni*), occur in Britain, chiefly in mountain districts. The geographical distribution of these species is very remarkable. They are plants of the Southern Hemisphere with a wide distribution in Australia, South Africa and South America, reaching Europe through the Canary Islands and extending (*H. wilsoni*) as far as Norway. This extraordinary northward extension of their range is marked by a very strict selection of habitats, for in Western Europe they are confined to the most sheltered habitats, in districts with the most equable climate. The species concerned are very closely related and are possibly no more than varieties of one form.

FIG. 509.—*Hymenophyllum tunbridgense.* Complete plant showing rhizome and leaves. About half natural size.

The stem is very slender, rarely more than 6 in. long and often much shorter, and bears two ranks of leaves which vary from 1 to 12 in. in length (Fig. 509). In outline the leaves vary from entire, with pinnate venation, to highly divided leaves which may be once, twice or thrice pinnate. There is a good deal of webbing, the lamina running decurrently along both the main raches and those of the pinnae, forming a narrow, continuous membrane. The filmy texture is a very marked characteristic, the laminae being translucent and for the most part only one cell thick, which probably accounts for the preference shown by these plants for moist and shady habitats. A few forms which occur in drier places have a covering of felted hairs, but there are no true ramenta.

The internodes of the stem are relatively long, and branching is carried

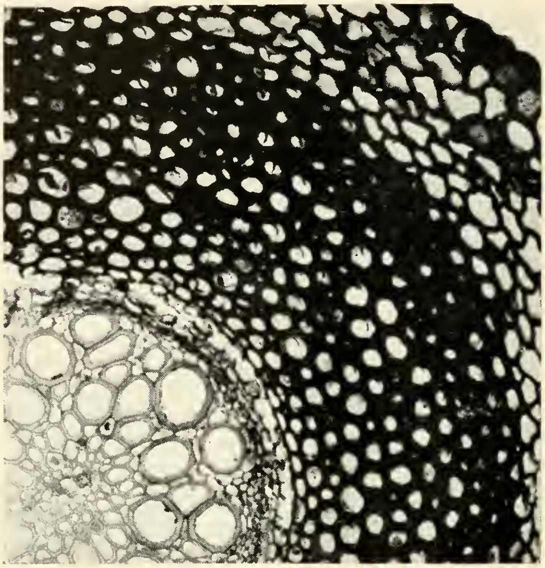

FIG. 510.—*Hymenophyllum tunbridgense.* Transverse section of rhizome showing protostele with central protoxylem and thick-walled cortex.

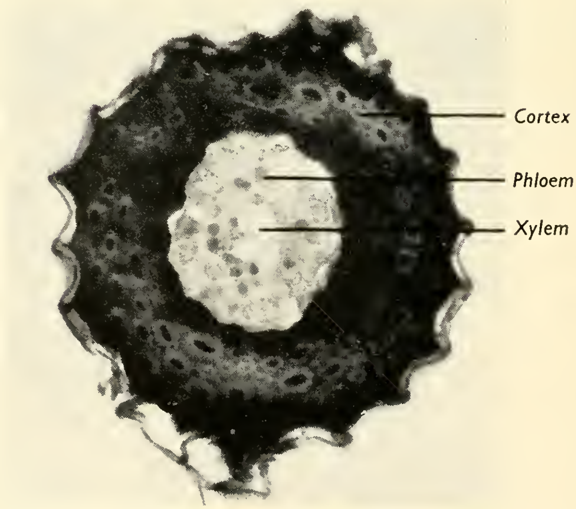

FIG. 511.—*Hymenophyllum tunbridgense.* Transverse section of the petiole showing heavily thickened cortex and collateral stele.

out by axillary buds, developed at the nodes, of which the majority remain dormant. Axillary buds are rare among Ferns, and it has been suggested that in this instance the axillary bud is really the weaker or suppressed branch of a dichotomy of the main stem, and that the leaf is really the first leaf of this branch. On the other hand, a comparison with Ferns which show equal dichotomy leads to a different interpretation. In dichotomies with equal branching there is always present a leaf which stands at the point of forking and is called the **angular leaf.** Such leaves are characteristic of Ferns and do not occur in Lycopodiales. When the two branches are somewhat unequal, the angular leaf is often shifted on to the weaker branch, as in *Pteridium.* This may be the case in *Hymenophyllum*, and the leaf may be really an angular leaf between the main branch and the side branch.

The Filicales show no such fixed relationship between branch and leaf as obtains in the Angiosperms. The evolutionary trend has been from dichotomy towards true axillary branching and in the Filicales the arrangement is still fluid. Lateral branches may arise on either side of the leaf-insertion, or in the leaf axil, or below the leaf, or finally, the branch may be shifted on to the leaf itself or the leaf on to the branch. There is thus great diversity, illustrating the course of evolution towards the fixed type of axillary branching, which was attained at an early stage in the Equisetales but not in the Filicales or their immediate relations. The angular leaf at a dichotomy is, however, clearly the prototype of the subtending leaf of an axillary branch, and the whole tendency of evolution has been to fix the branching system in relation to particular leaves.

Anatomy of the Stem

There is a broad cortex which shows a thin-walled outer zone and a thick-walled, dark-coloured, inner zone. The single, central stele is delimited by a typical endodermis, within which is a pericycle of one to several layers of thin-walled cells (Fig. 510). The xylem forms a central core, surrounded by a continuous phloem. The xylem is solid, with central protoxylem, and is therefore protostelic. A small number of parenchyma cells are scattered among the tracheids towards the centre of the stele and may, in some large species, be aggregated into a ring which separates the protoxylem from the metaxylem.

The protoxylem and some tracheids of the metaxylem form a simple collateral strand in the leaf trace, which naturally leaves no gap in the stele. In the rachis this strand widens into a more or less curved arc (Fig. 511).

Anatomy of the Leaf

The lamina is formed of one layer of cells only, except in a few species, and has the delicate translucent texture of a Fern prothallus (Fig. 512). It is sensitive to bright light and to low atmospheric humidity and prefers moisture and deep shade. The venation of the leaves is branched and open, without fusions, and normally each lamina segment receives one vein. The reduced character of the genus is shown by the presence of pseudo-veins, consisting of sclerenchyma cells without any vascular tissue, which either take the place of the regular veins or form direct prolongations of them. They are obviously imperfect veins and can hardly be anything but reduced structures.

There are naturally no stomata in a single-layered lamina, and the cuticle of the cells is extremely thin. On the other hand, the side walls are thick and strongly pitted. Contrary to the behaviour of other plants, *Hymenophyllum* can absorb water through its leaves. The lamina cells are very permeable, and a drop of water placed on the leaf surface does not readily run off but spreads and sinks into the cells. This capacity must be of great importance to the smaller rootless species, whose vascular strands are so much reduced that it would be virtually impossible for the water supply of the whole plant to pass along them. The saturated air and heavy rainfall of the tropical rain forest seem indeed to have induced in *Hymenophyllum* characters which are those of a semi-aquatic plant.

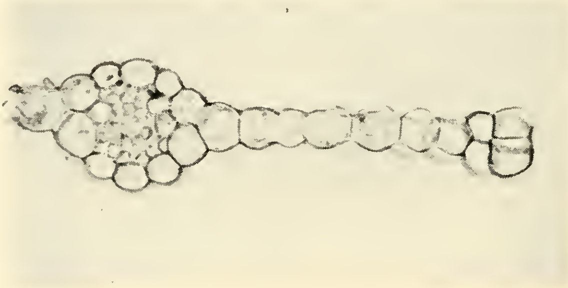

FIG. 512.—*Hymenophyllum tunbridgense.* Transverse section of the lamina of a pinna showing midrib and thickened margin.

The leaf margin is often formed of sclerotic cells, recalling the leaf margin in some Mosses like *Mnium*. This serves the double purpose of preventing tearing of the lamina and of keeping it taut, like the skin of a drum, thus preventing the flaccid drooping which would be inevitable in so thin a structure if it were not mechanically stiffened. The leaf veins contain a very small number of vascular elements, but each is surrounded by a sclerotic sheath which is an important reinforcement of the lamina.

The growth of the young lamina is quite different from that of other Leptosporangiatae. The margin consists of a continuous row of narrow cells, shaped like half-discs, arranged side by side. These cells only divide parallel to their inner, flat faces, thus building up the single layer of cells. In the lowest part of the leaf the segmentation of the marginal cells by alternating oblique walls, which is characteristic of other Ferns, may occasionally be seen, but in the members of the Hymenophyllaceae which have thicker leaves, *e.g.*, *Trichomanes reniforme*, the leaf is still built up from a margin of half-disc shaped cells, the increased thickness being acquired by subsequent periclinal divisions of the lamina cells. This suggests that these thickened leaves have been secondarily evolved from the usual one-layer type.

SORUS AND SPORANGIA

The sori are marginal and stand at the tips of certain of the leaf veins, which are prolonged beyond the edge of the leaf in the form of a **receptacle,** the equivalent of the placenta in *Dryopteris*, on which the sporangia develop in basipetal succession. The sorus is enclosed in an indusium (Fig. 513), consisting of two equal and distinct lobes or valves, which arise from the upper and lower sides of the lamina respectively, on each side of the receptacle. In some species the latter extends by intercalary growth beyond the indusial covering, so that only the lower part of the sorus, where the young sporangia are forming, is protected by the indusium. The older sporangia near the top of the receptacle project into the air and are thus better situated for spore dispersal. The indusium is hygroscopic and closes against the sporangia in dry weather. Finally it withers and dries up at the time when the lowest sporangia are mature and ready to shed their spores.

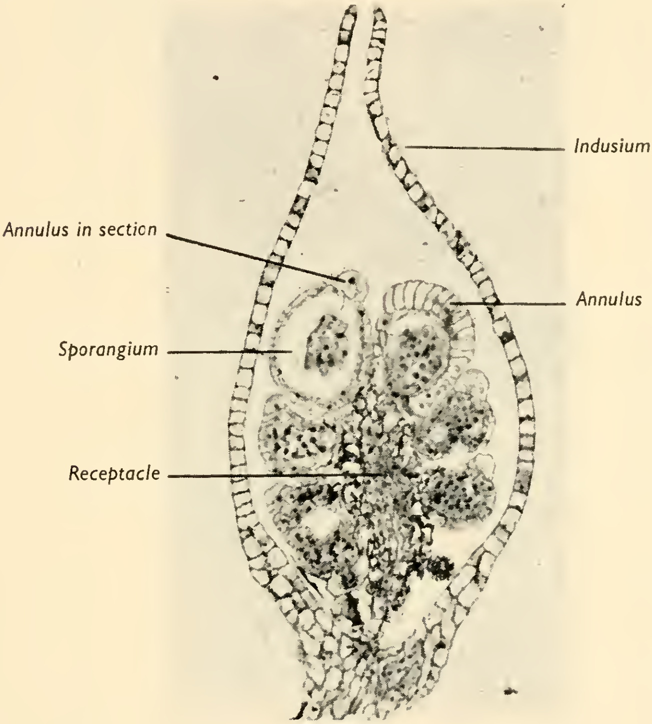

FIG. 513.—*Hymenophyllum tunbridgense.* Section through sorus showing cup-shaped indusium and sporangia developing successively from apex to base of the receptacle.

The early development of the sporangia does not differ essentially from that in other Leptosporangiatae. The ripe sporangia are broadly rounded and are almost sessile on the receptacle. They have a well-developed annulus which, however, differs from that in *Dryopteris*, *Pteridium* and other Polypodiaceae in being oblique, that is to say, it does not lie in the plane which intersects the point of attachment of the sporangium but lies obliquely across it, bisecting the sporangial wall into two unequal halves (Fig. 514).

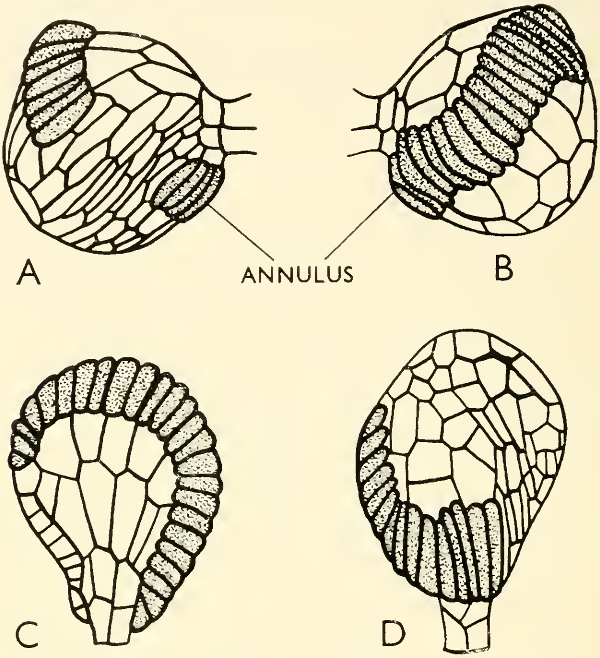

Fig. 514.—*Hymenophyllum tunbridgense.* Sporangia showing broad oblique annulus. (*After Bower.*)

The annulus is a complete circle of uniform cells, only those at the stomium, or point of dehiscence, being as a rule somewhat smaller than the rest. The number of spores in each sporangium is always greater than that in the Polypodiaceae, but is variable, in different species, between 128 and 512, numbers which mark the group as related to the primitive Ferns called by Bower the *Simplices*, in which the spore numbers are always high.

The Gametophyte

The prothallus consists of a number of green, branched, strap-shaped lobes, one cell in thickness, with a slight increase in thickness at the points on the margins where the antheridia and archegonia are developed (Fig. 515). Its appearance recalls the thallus of some Bryophyta of the Jungermanniales. The earliest stage of the prothallus is the development of a short filament of five or six cells, as in *Dryopteris*, but in *Trichomanes* the whole prothallus is filamentous. In *Hymenophyllum* a short-lived apical cell is formed, from which the first broadening of the prothallus originates, but this soon gives place to an apical meristem and marginal growth. Branching is brought about by the dichotomy of the apical meristem, followed by unequal growth of the two limbs, so that the weaker of the two looks like a side shoot. Rhizoids are produced in marginal groups.

Gemmae are a peculiar feature of the prothallus in this family. In *Hymenophyllum* they develop from the margin in the form of little flat plates of cells, provided with an apical cell, very like the young stage of the prothallus itself. They are detached and form a means of vegetative propagation of the prothallus.

Antheridia and archegonia are borne in closely set groups on the under sides of lobes of the thallus, which are really specialized branches formed by the dichotomy of the prothallus apex. Such fertile lobes may be produced at intervals over a considerable period of time. The filaments of the *Trichomanes* prothallus develop the archegonia in groups on very short branches which are called archegoniophores and which probably correspond to the fertile lobes in *Hymenophyllum*. The gametangia do not differ essentially from the usual Fern type, nor does there appear to be anything peculiar in the embryogeny, so far as it is known.

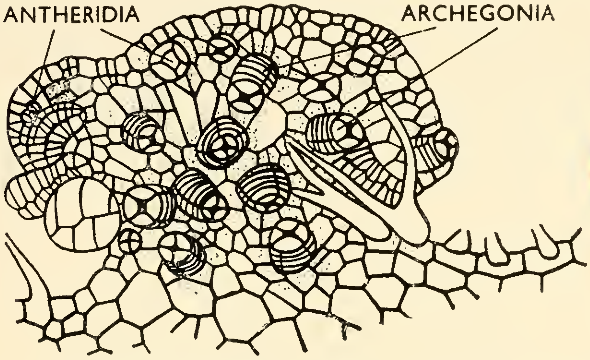

FIG. 515.—*Hymenophyllum dilatatum.* Lobe of the prothallus with antheridia and archegonia. (*After Goebel.*)

Leptosporangiatae: Osmundaceae

The Osmundaceae are a small family of Ferns, of great interest both on account of their peculiar morphology and of their fossil history, which is unusually well known. There are two genera, *Osmunda* with nine species and *Todea* with only one, though a third genus, *Leptopteris*, with seven species is sometimes united to *Todea*.

The outstanding character of the group is the structure of the sporangium, which has only a rudimentary annulus consisting of a group of thick-walled cells at one side, while the dehiscence follows a line across the sporangial apex. The sporangia are large, are not constant in regard to their formation on the leaf margin or the leaf surface and are not grouped in sori or protected by an indusium. Furthermore they develop more or less simultaneously. All these are primitive characters and justify the inclusion of the family in Bower's *Simplices.*

The Osmundaceae occupy an intermediate position between the Leptosporangiatae and the Eusporangiatae, though they are usually included in the former group. This indeterminate position is due to the variations in the development of single sporangia, even on the same plant, some forming a pyramidal archesporial cell, as in the Leptosporangiatae, others a cubical cell, as in the Eusporangiatae. The sporangia are derived from more than one cell of the sporophyll which is a character of the latter group.

The Ferns of this family are mostly large plants with perennial stems, which are embedded upright in the soil with only the crown exposed. They may branch dichotomously in old specimens and form large masses of stems up to a metre in diameter and sometimes several feet in height. The leaves are deciduous and when they die down in autumn they form a blanket over the crown of the plant, persisting through the winter in the dry state.

The Osmundaceae occur in all parts of the world, but *Todea* is confined to South Africa and Australia. In the tropics *Osmunda* is confined to mountain ranges and does not grow at lower levels. They extend backwards in time to the Palaeozoic period, and were well developed in the Jurassic. They show connections with a primitive group of Ferns, the Botryopteridaceae, which were abundant in the Carboniferous, and they have probably been derived from them.

In *Todea* the fertile leaves are morphologically identical with the sterile leaves, but in *Osmunda* the fertile upper pinnae of the leaves have practically no lamina and bear sporangia all round, thus appearing very different from the lower sterile portions, which has led to their being popularly called "Flowering Ferns."

We shall describe as a type the species *Osmunda regalis.*

Osmunda regalis (The Royal Fern)

Osmunda regalis is a native of Britain, being found in boggy places chiefly in the moist regions of the West and North. It is not uncommon, but seldom occurs in large numbers. It has a wide geographical range, from Sweden to South Africa and from Canada to the Argentine. The plant is perennial and grows to a large size, with leaves which may be up to 6 ft. long (Fig. 516). They last only for one season, but their bases remain as persistent coverings around the stem, as in *Dryopteris.* There are distinct sterile and fertile leaves, and the latter are produced first and stand erect, while the sterile leaves arch outwards around them (Fig. 517). Each leaf is bipinnate, and in the fertile leaves the five or six pairs of pinnae nearest the top of each leaf are reduced to little more than their midribs and bear masses of brown sporangia all over their surfaces, which makes them rather conspicuous objects.

FIG. 516.—*Osmunda regalis.* Plant showing sterile and fertile fronds. Much reduced.

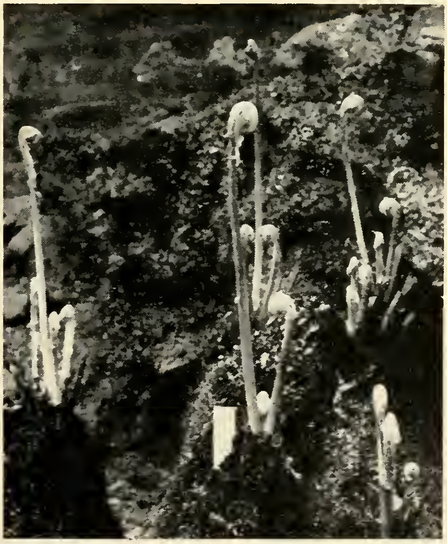

FIG. 517.—*Osmunda gracile.* Developing fertile leaves showing circinate vernation.

ANATOMY OF THE STEM

The stem of the young sporeling plant is protostelic, but as it matures the stele becomes medullated and the ring of vascular tissue is finally broken into a number of separate strands, which are often U-shaped, with the arms pointing inwards. The parenchymatous intervals between these strands are leaf gaps, but the arrangement is not truly dictyostelic, because there is a common endodermis surrounding the entire ring, and the strands are therefore not meristeles but only portions of a broken ring (Figs. 518 and 519).

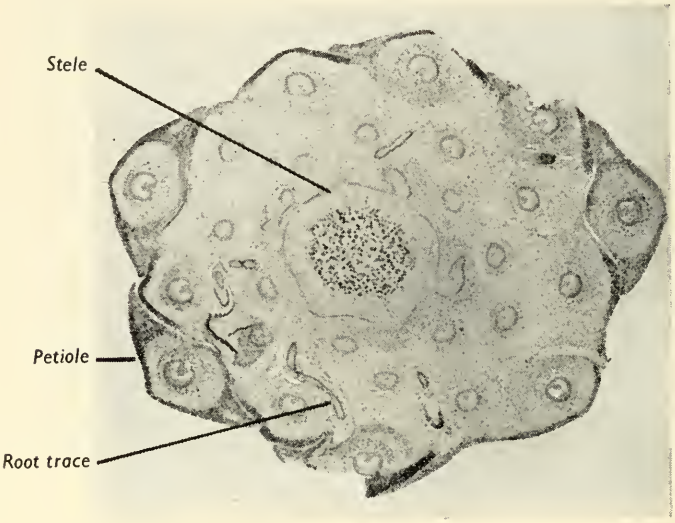

Fig. 518.—*Osmunda regalis.* Transverse section of entire stem showing central stele with pith, leaf traces and at the periphery, separated leaf bases.

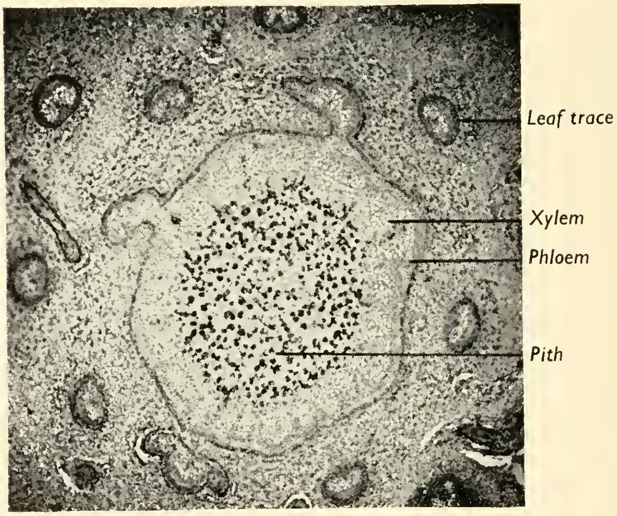

Fig. 519.—*Osmunda regalis.* Enlarged view of stele in Fig. 518 showing the separation of the leaf traces from the stele.

This arrangement is unique among living Ferns and has been compared with the ring of vascular bundles in a dicotyledonous stem. The comparison is, however, purely superficial, for there is a continuous ring of phloem, which is in fact broader and better developed between the xylem strands than opposite them, as it is in a true vascular bundle. A further peculiarity is that the endodermis does not open at the passage of the leaf trace from the stele to the cortex. This is brought about by the union of the endodermis which surrounds the leaf traces with that which surrounds the stele, at the point of contact between the two, so that at no place, except occasionally at the base of a branch, is there any uninterrupted continuity between the medulla and the cortex. The protoxylems are usually mesarch, but lie towards the outside of the xylem groups (Fig. 520). The phloem is distinguished by the presence of numerous sieve tubes, the perforations of which contain callus strands, a rare thing in the Pteridophyta, and are covered by minute slimy globules of uncertain nature. Around the phloem lies the pericycle, consisting of three or four layers of thin-walled cells, and outside this is the endodermis with rather irregularly suberized walls. *Osmunda regalis* has only one endodermis, but in *O. cinnamomea* there is an inner endodermis, though it is somewhat irregular and not always complete.

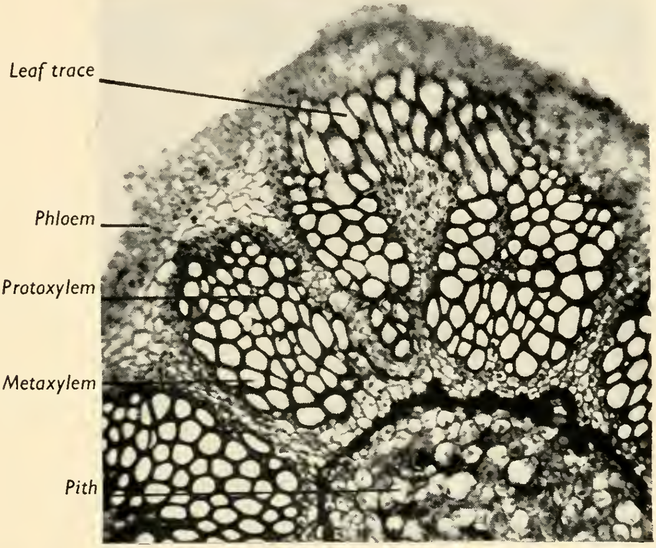

Fig. 520.—*Osmunda regalis.* Vascular tissues of stele showing mesarch protoxylems.

The stele of *Osmunda*, when dissected out and viewed from the side, shows that the spaces between the xylem masses are really very elongated leaf gaps, so that the whole structure is analogous to a true dictyostele, except for the presence of the single sheathing endodermis (Fig. 521). The scalariform xylem elements have been shown to be in open connection with one another and must therefore be reckoned as vessels, not simple tracheids (cf. *Pteridium*, p. 509).

ANATOMY OF THE PETIOLE

When an entire stem of *Osmunda* is cut across transversely it will be seen that the actual stem tissue occupies only about one-seventh or less of the entire section, and the rest is made up of a mass of closely packed leaf bases, arranged in a spiral sequence. Each leaf base contains a petiolar stele surrounded by a dark-brown band of sclerenchyma, outside which is a broad parenchymatous cortex, lozenge-shaped in section. The soft outer tissues are so closely packed together around the stem that their limits are difficult to distinguish in the mass, and they give the appearance of a continuous tissue, which might be mistaken for an extension of the stem cortex.

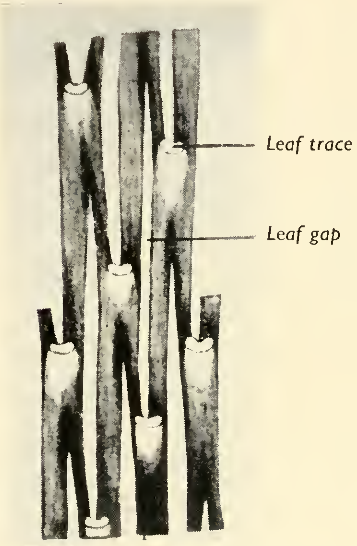

FIG. 521.—*Osmunda regalis.*—Portion of the stele dissected out to show dictyostelic structure. (*After Kidston and Gwynne Vaughan.*)

Close to the base of each petiole two adventitious roots are given off, which wind their way outwards between the leaf bases and on emerging form a tangle around the outside. The stele in each petiolar trace passes downwards and inwards through the true cortex of the stem and enters the stele as a horseshoe shaped mass of phloem and xylem, the latter having one protoxylem on its inner concave side. It passes into the ring and takes its place there at the base of a gap. Below the point of junction of leaf trace and stele two of the stelar bundles fuse to form the trace, and this is the origin of its curved outline. The xylem of the trace is composed, unlike the stem xylem, of scalariform tracheids, and is surrounded by a zone of phloem and an endodermis. This is surrounded by a parenchymatous inner cortex, followed in turn by a sclerenchymatous band and the parenchymatous outer cortex already referred to. Close to the actual stem the sclerenchyma of the separate petioles becomes fused into a solid mass, which is of great hardness and very difficult to cut.

ANATOMY OF THE ROOT

The cortex is very broad relative to the stele, and consists of cells which are thin-walled near the endodermis and become progressively thicker-walled outwards (Fig. 522). The stele is protostelic, with a diarch or triarch xylem, separated from the phloem by several layers of parenchyma, and surrounded by a two-rowed pericycle and an endodermis.

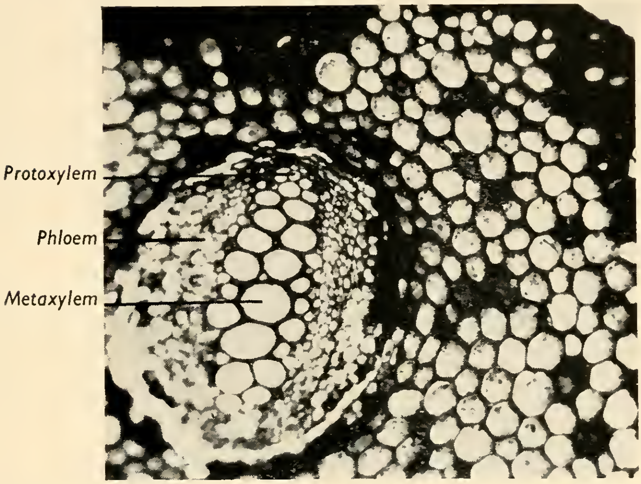

Fig. 522.—*Osmunda regalis.* Transverse section of the root showing diarch xylem.

Anatomy of the Leaf

The base of the petiole forms part of the structure of the stem and has already been described. As the leaf trace ascends the petiole it becomes broader and opens out into a C-shaped band, with the arms directed adaxially and the edges incurled (Fig. 523). The protoxylem divides into several groups, arranged along the concave face, alternating with groups of mucilage cells. A narrow phloem mantle and a continuous endodermis surrounds the whole strand. When a pinna trace is given off the petiolar strand broadens

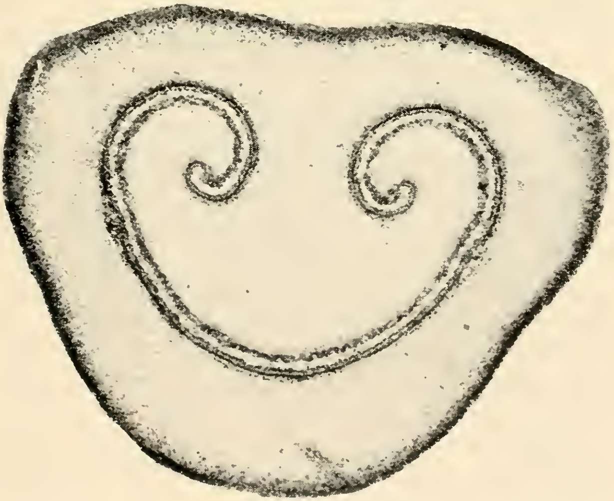

Fig. 523.—*Osmunda regalis.* Transverse section of the petiole showing C-shaped vascular strand.

and becomes flatter. A loop begins to bulge out at one side, becomes more and more curved and detaches itself from the main bundle, first at one edge, then at the other. This leaves a small gap in the curve of the main strand, which is rapidly closed by its edges coming together. Meanwhile the loop moves off to the base of the pinna, its curved face at first turning towards the main petiole. The petiole of the pinna is twisted at right angles close to its base so that its lamina lies in a line with the main petiole and thus the whole frond is flat in appearance, though morphologically the plane of each pinna is horizontal, not vertical as in other Ferns.

The leaves are as a rule broadly bipinnate in the mature state, though the youngest leaves in the sporeling state are ternate and the mature form is only gradually acquired. Each pinnule is attached by a short, narrow stalk and has a single midrib with pinnate veins on both sides, which do not anastomose. The structure of the sterile lamina agrees with the ordinary *Dryopteris* type. There is no palisade layer, though the mesophyll is denser towards the upper side and more lacunar towards the under side, on which are numerous stomata.

FIG. 524.—*Osmunda regalis.* Fertile frond showing upper sporangiferous pinnae and lower vegetative ones.

The pinnae are set more or less regularly in opposite pairs. The uppermost half-dozen pairs are usually wholly fertile (Fig. 524), but intermediate stages occur in the pinnae immediately below this level, which may be partly fertile and partly sterile. Among their pinnules there are often to be found some in which the lamina is reduced but which bear only the rudiments of abortive sporangia.

The wholly fertile pinnules are reduced to little more than the width of their midribs and bear two naked, marginal masses of sporangia which, when mature, completely conceal the pinnules and give the impression of covering their entire surface. This is an important distinction between *Osmunda* and

Todea, for in the latter the sporangia are superficial on the lower surfaces of unmodified pinnules. The absence of separate sori and the difference of sporangial position in the two genera emphasizes the primitive character of the family.

The leaf of *Osmunda* grows by means of a three-sided apical cell, which is exactly like that of the stem (Fig. 525). This is in contrast with the two-sided apical cell which is common to the leaves of most of the Leptosporangiatae, and it is in accord with the large size and robust structure of the leaf. The lamina does not grow from a single row of marginal initial cells, as in the Leptosporangiatae, but has a massive, marginal, meristem tissue with segmentation of a complex type, which may be derived from a double row of initial cells.

The similarity of the apical region in the leaf and the stem lends special interest to the observations of Lang, that in starved plants of *Osmunda* very much reduced leaves may be formed, which appear as short cylindrical growths without a lamina. On these abnormal growths buds may appear at various levels, or the apices may be directly transformed into buds which develop normal leaves in regular succession. The actual transformation of a leaf into a shoot is a very unusual phenomenon, and it has been suggested by Wardlaw that there has been here, as in *Dryopteris*, a shifting of a branch apex, laterally, on to a leaf rudiment. In the latter Fern a bud normally appears high up on the abaxial side of the petiole, and in the *Osmunda* leaves it may have reached the leaf apex and apparently replaced it.

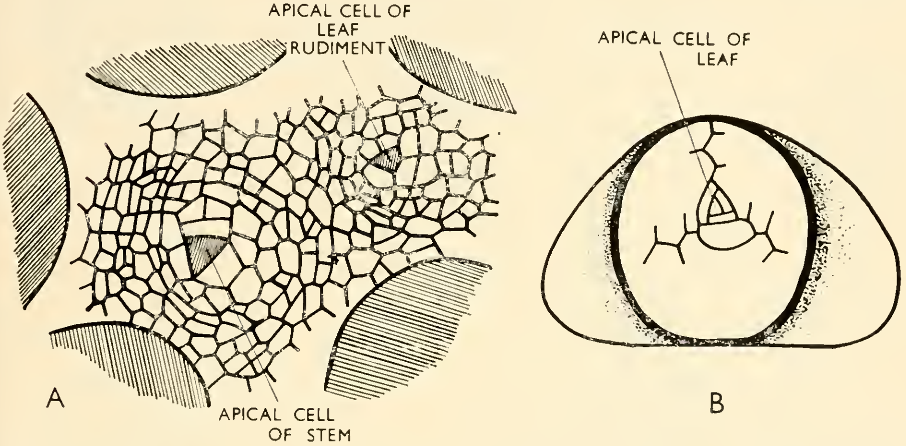

Fig. 525.—*Osmunda regalis*. A, Apex of stem showing origin of leaf rudiment. B, *Osmunda cinnamomea*. Apex of young leaf, before pinna formation, showing apical cell and stipular expansions of leaf base. (*After Bower*.)

Development of the Sporangium

When the sporangium first becomes visible as a small protuberance on the fertile pinnule there is a conspicuous **initial cell**, but several cells take part in the formation of the sporangium, especially in that of the stalk. It is therefore not strictly Leptosporangiate. The initial cell is usually pyramidal, but cubical cells are also to be found, and these latter are plainly similar to the archesporial cells of that shape which are to be found in the Eusporangiatae (Fig. 526). The initial cell divides into two horizontally, cutting off a **primary wall cell** above and an **archesporial cell** below. The wall cell divides anticlinally to form a single layer of wall cells. The archesporial cell also divides parallel to all its faces and cuts off a second series of peripheral cells, which form an inner layer of the wall. The remaining central cells divide repeatedly and produce a mass of **sporogenous cells,** the outer layer of which becomes the **tapetum,** which later breaks down into a plasmodium, and penetrates between the developing spores. The cells of the floor of the sporangium may also contribute to build up this tapetum, a procedure which again recalls the Eusporangiatae. The sporangia are normally single, but synangia sometimes occur. The fertile sporogenous cells function as spore mother cells and undergo meiosis to produce spores. The number formed is always large, but appears to be variable, counts between 256 and 512 being recorded.

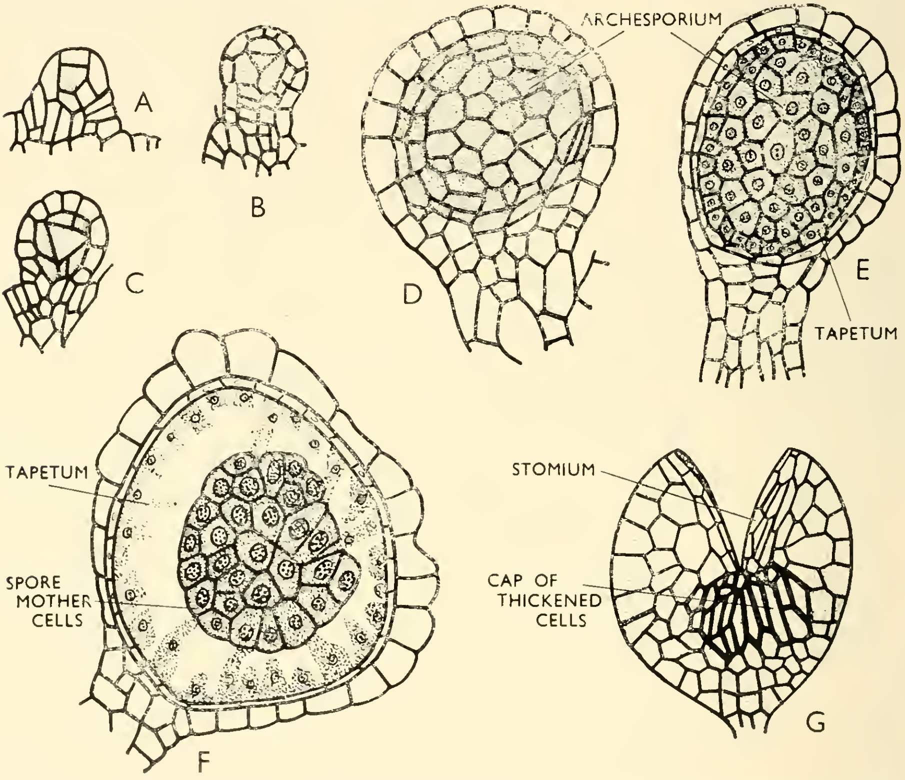

FIG. 526.—*Osmunda regalis.* Development of sporangium. A to C, Origin from a group of cells, showing cubical and pyramidal archesporial cells. D and E, Development of archesporium. F, Spore mother cells. G, Dehiscent sporangium showing cap of thickened cells. (A *to* D *after Bower,* E *to* G *after Smith.*)

The mature sporangium is more or less spherical, with a thick stalk (Fig. 527). The wall is one layer thick and is marked across the top of the sporangium by a double row of narrow cells, the **stomium,** along which the sporangium dehisces. There is no true annulus, but at one side there is a group of thickened cells which may be supposed to represent it. This cap-like annulus has been held to be a reduced remnant of a multiseriate annulus of the *Botryopteris* type. The spores contain chloroplasts when ripe and germinate immediately. They are unable to survive for long after being shed.

Fig. 527.—*Osmunda regalis.* Transverse section of sporangiferous pinnule showing the rachis bearing a cluster of sporangia with thick stalks.

The Gametophyte

When the spore germinates the extine breaks along a triradiate ridge, formed by the compression of the spores into tetrads in the sporangium. The spore contents emerge and elongate into a cylindrical cell which divides transversely into two unequal portions. The smaller of these develops into the prothallus, while the larger becomes the first rhizoid, which, unlike those of other Ferns, contains chloroplasts. The prothallial cell first forms a row of cells, of which the terminal cell organizes itself by oblique divisions into a pyramidal apical cell, and proceeds to build up the prothallus. Later on it is replaced by a four-sided cell, and still later by a group of similar cells, as in *Dryopteris.* The resulting mature prothallus has the same cordate shape as in the Leptosporangiatae (Fig. 528), but is rather larger and more massive and continues its growth for several years, resembling the dark green thallus of one of the Jungermanniaceae. It may eventually branch, and adventitious budding is not uncommon, as in the Marattiaceae.

Sexual development begins with the formation of antheridia, which appear on the young prothalli before the archegonia.

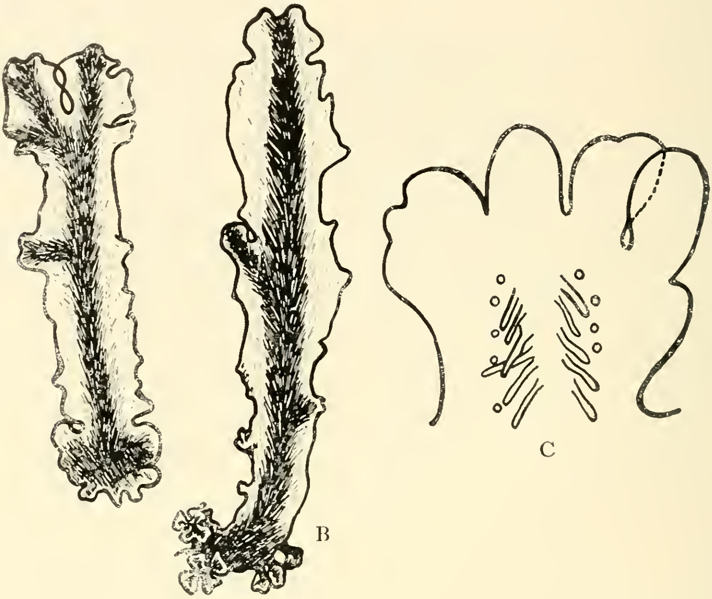

FIG. 528.—*Osmunda regalis.* Prothalli showing prolonged growth and adventitious budding at base of B. C, Lower surface showing rhizoids and position of archegonia. (*After Goebel.*)

DEVELOPMENT OF THE ANTHERIDIUM

The antheridia are borne marginally in young prothalli and also ventrally on the wings in later stages. A single cell grows out beyond the general level of the neighbouring cells, and its protruding apex is cut off by an oblique wall. A second oblique wall, intersecting the first, cuts off a pyramidal apical cell, which by further divisions may add to the lower cells first formed, and builds up a short **pedicel,** which raises the antheridium still more above the prothallus surface. The apical cell now divides transversely and cuts off a wall cell at the top, from which other wall cells are produced, thus enclosing the apical cell, which then divides to form antherozoid mother cells. The whole antheridium is much larger than that in *Dryopteris*, producing more than a hundred antherozoids. The wall is likewise formed of more cells than is normal in the Leptosporangiatae, and it opens by throwing off a small triangular **opercular cell** either at the apex or at the side, which resembles the opercular dehiscence in the Eusporangiatae. The antherozoids are not essentially different from those of *Dryopteris.*

DEVELOPMENT OF THE ARCHEGONIUM

The archegonia develop on the under side of the central rib or thickened cushion of cells. They appear only on the sides of this rib and stand horizontally, that is to say, with the necks roughly parallel to the lower surface of the prothallus. The details of their development are essentially similar to those of the archegonia in *Dryopteris*. There is, indeed, a marked constancy in the development of the archegonia all through the Ferns. In *Osmunda* the chief differences are that the neck is eight tiers long and is straight, not bent.

DEVELOPMENT OF THE EMBRYO

Only one embryo comes to maturity on each prothallus, though several may begin development. The first two divisions of the oospore are parallel to the axis of the archegonium and at right angles to each other, while the third is transverse and cuts across the first four cells to form an octant. The further development is exceptional in that the stem, root and first leaf are all derived from one-half of the octant, while the other half only forms the foot. The latter organ is much larger than is usual in the Leptosporangiatae and penetrates deeply into the prothallus, forming **haustorial cells** over its surface, like the foot of the sporophyte in *Anthoceros*. The embryo develops its parts slowly and remains for a considerable time a mere globular mass, and the cotyledon does not break out of the archegonial wall until comparatively late in development (Fig. 529). All these are relatively primitive

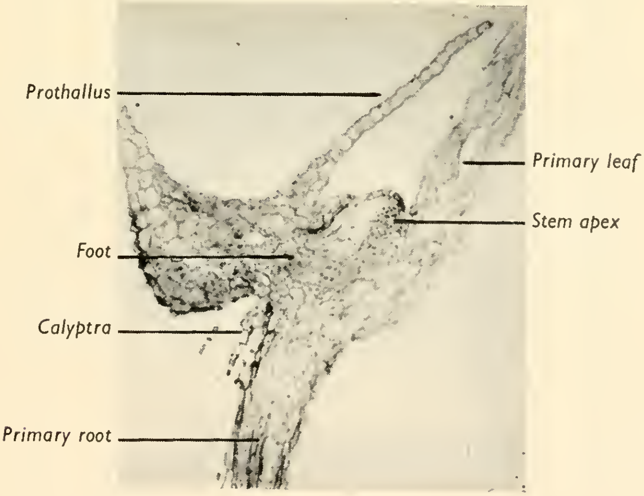

FIG. 529. — *Osmunda regalis*. Vertical section of the prothallus and attached embryo.

characters, more closely resembling the Eusporangiatae than the Leptosporangiatae. The first leaf does not, however, penetrate the prothallus, but grows up round its side, which is a character of the latter group.

Apogamous embryos have been observed in *Osmunda*, formed by a meristem which originates on the under side of the central cushion of the prothallus. Such embryos are formed without any union of gametes taking place, but a fusion of vegetative cells may occur, giving a diploid sporophyte, as in the normal case.

Relationships

We have remarked above that the Osmundaceae have a fossil history going back to the Palaeozoic period. The fossil representatives were fully investigated by Kidston and Gwynne Vaughan, who showed that the peculiar dictyoxylic stele of the living types was derived from an early protostelic condition by the development of a parenchymatous pith. Early traces of this change can be seen in the differentiation of the xylem mass into an outer zone of conducting elements and a central core of short storage tracheids, a condition shown in the Permian types *Zalesskya* and *Thamnopteris*. A further stage in the change is shown by *Osmundites kolbei* from the upper Jurassic, which has a " mixed pith " consisting of parenchyma with scattered tracheids, obviously an indication of the progressive parenchymatization of the central part of the stele. The Palaeozoic types have broad zones of wood with no leaf gaps, but the Mesozoic *Osmundites* has developed gaps corresponding to those in the living genera, associated with a much-narrowed xylem zone. As Bower points out, the living *Osmunda* has preserved the condition arrived at by the family in Jurassic times, while *Todea* corresponds rather to the Cretaceous types of *Osmundites*. The change of stem structure has been accompanied by an expansion in diameter and opening out of the stele as a whole, which is apparently correlated with increasing size of the plants.

The Osmundaceae as a family probably stand closest in relationship to the protostelic Botryopteridaceae. The main difference between the two families so far as the vascular anatomy of the stem is concerned lies in the position of the protoxylem, which is mesarch in Osmundaceae and endarch in Botryopteridaceae. The older species of *Botryopteris* showed also some degree of mesarchy in the leaf trace, a condition corresponding to that at the base of the petiole in *Thamnopteris*. The probable relationship of the sporangial structure in the two families has already been touched upon. There is good reason for the suggestion that the two families Osmundaceae and Botryopteridaceae are related and have probably been derived from a common ancestry (see Volume III).

We may perhaps usefully summarize very briefly the points in which *Osmunda* shows a primitive condition :—

1. Dichotomy of the main axis.
2. The three-sided apical growth of the leaves and the thick marginal meristem of the lamina, together with the open venation.

3. The medullated, monostelic, vascular structure of the stem.
4. The absence of distinct sori and of indusia.
5. The irregularity of the divisions at the early stages of sporangial development.
6. The large sporangia, with no proper annulus and with a relatively large spore output.
7. The massive and long-lived prothallus.
8. The complex wall system and large size of the antheridia.
9. The slow development of organs in the embryo.

Eusporangiatae: Marattiaceae

The Marattiaceae are distinguished by the massive sporangia which originate from a group of cells, not from a single cell, as in the Leptosporangiatae. They are correspondingly robust in all their parts; the stems are solid and almost tuberous, the petioles thick and long, and the leaves large and leathery.

Marattia fraxinea

Species of *Marattia* are very large Ferns, native to both Eastern and Western Tropics, and often cultivated as hothouse plants (Fig. 530).

FIG. 530.—*Marattia fraxinea.* Plant growing at Kew Gardens. Much reduced.

Marattia fraxinea is one of the most widely distributed species, occurring as far south as New Zealand.

The stem is about 10 cm. high and the same in thickness. The petioles are about 50 cm. long and 2 to 3 cm. thick. The leaf blade may be a square metre in total spread, but it is compound and two to three times pinnate (Fig. 531). Each pinnule is shortly stalked, lanceolate in outline and measures 2 to 3 cm. broad by 15 cm. long. Each pinnule has a strong midrib with free lateral veins, which fork once, each fork supplying a sorus near the margin. At the base of each petiole there are two thick **stipules,** which are generally united (Fig. 532). The leaves are eventually separated from the stem by an **abscission layer** just above the stipules, which remain attached as a permanent covering of the old stem.

Fig. 531.—*Marattia fraxinea.* Part of a fully developed leaf. The original is about 1 metre across.

The petioles of *Marattia* have a large number of leaf trace bundles arranged in a complex pattern, which is fundamentally that of an arch with its open side towards the stem. Only two bundles enter the leaf base from the stem (cf. *Cycas*, p. 716), each with a single central protoxylem, and the numerous meristeles of the petiole are produced by the branching of these two.

Anatomy of the Stem and Leaf

The stem apex shows a **meristem,** not a single apical cell, though there is some evidence that a group of four apical cells is involved in the formation of the meristem. A single apical cell exists only in the sporeling.

The stem of the sporeling is protostelic, but in the mature stem there is a very complex polycyclic dictyostele of numerous small meristeles, which is rendered more complex by the frequency of commissural strands linking together the various vascular rings into a three-dimensional lattice, also by the departure of very numerous leaf traces from the outer vascular zone, and by the multiplicity of adventitious root traces which come from the outer and inner zones (Fig. 533). In spite of this it is recognizably a compound dictyostele of the *Pteridium* type, differing only in the much greater degree of dissection of the stele. A noteworthy peculiarity is the absence of an endodermis, except in the young plant.

FIG. 532.—*Marattia fraxinea.* Very young plant showing stipules attached to leaf bases. Natural size.

The commissural strands appear to be downward continuations of the incoming leaf-trace bundles. Each of them leaves the outer stele at the top of the leaf gap directly below that to which the commissural strand belongs, and it enters the inner stele at the base of a similar gap. The gaps in the inner stele may therefore be regarded as true leaf gaps, like those in the outer stele.

There is ground for believing that the whole vascular system in *Marattia* is a complex of leaf traces and that no truly cauline stele is present.

In the development of the young leaf the marginal row of initial cells typical of Leptosporangiatae is replaced by a band of meristematic tissue which is associated with the much thicker leaf blade of *Marattia.*

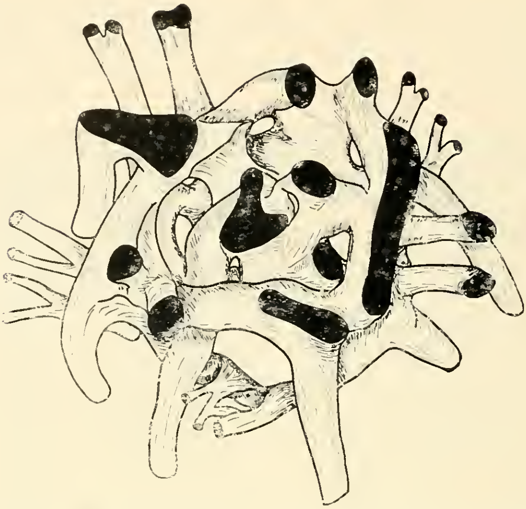

FIG. 533.—*Marattia fraxinea.* Dissected stele isolated from soft tissues. The black areas represent meristeles cut in transverse section. Several paired leaf traces may be seen arising around the periphery. (*After West.*)

ANATOMY OF THE ROOT

The root of *Marattia* differs greatly from that generally found in the Leptosporangiatae. It has a broad, soft cortex and a stele which contains about a dozen xylem strands, with external protoxylems, alternating with phloem groups (Fig. 534). As in the stem, there is no endodermis. The arrangement of the vascular tissue recalls that in a monocotyledonous root.

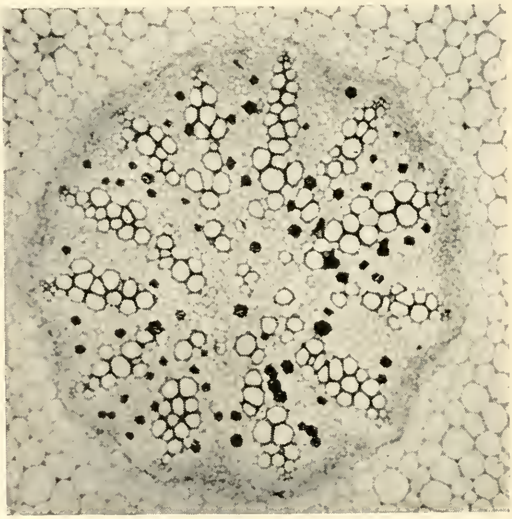

FIG. 534.—*Marattia fraxinea.* Transverse section of root showing polyarch structure.

Development of the Sporangium

Characteristic of the family as a whole are the sporangia, which have walls several cells thick, and are in *Marattia* united into solid, compound structures called **synangia** (Fig. 535). Each synangium is in two halves, like a small open pod, about 2 mm. long, with ten to twelve sporangia fused side by side in each half. The halves are at first closely pressed together, but when ripe they separate like an opening book (Fig. 536). The two halves are united beneath to a **placenta,** and below them arises a small membraneous **indusium** which never covers the synangium. Since the sporangia are completely united each sporangium appears only as a **loculus** in the compound structure, but each is individually much larger than the sporangium of a *Dryopteris* and produces about 2,500 spores as against forty-eight in the latter type. This large spore output is held by Bower to be a primitive character.

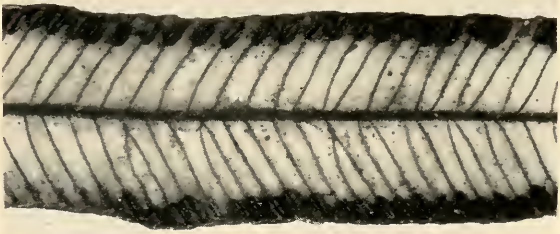

Fig. 535.—*Marattia fraxinea.* Portion of a fertile pinna showing marginal rows of synangia, each seated on a vein.

Fig. 536.—*Marattia fraxinea.* Section of pinna showing two mature dehiscent synangia.

There is no annulus and the sporangia dehisce along a ventral line of thin-walled cells, that is to say, inwards in the synangium.

The Gametophyte

The prothallus is larger and more solid than that of *Dryopteris*, though similar to it in form. The thickened cushion may extend almost to the margin. It may live for more than a year, growing and branching dichotomously, and if unfertilized will produce adventitious branches, which grow into secondary prothalli. An endophytic fungus is constantly present.

Development of the Antheridium

The antheridium develops from one epidermal cell which divides horizontally (Fig. 537). The inner cell forms the antherozoid mother cells and the outer cell divides by vertical walls to surround a small, central, triangular cell which is the operculum and is thrown off when the antheridium opens. The neighbouring prothallial cells cut off segments to form a wall round the mass of antherozoids. The whole antheridium is thus immersed in the prothallus tissue.

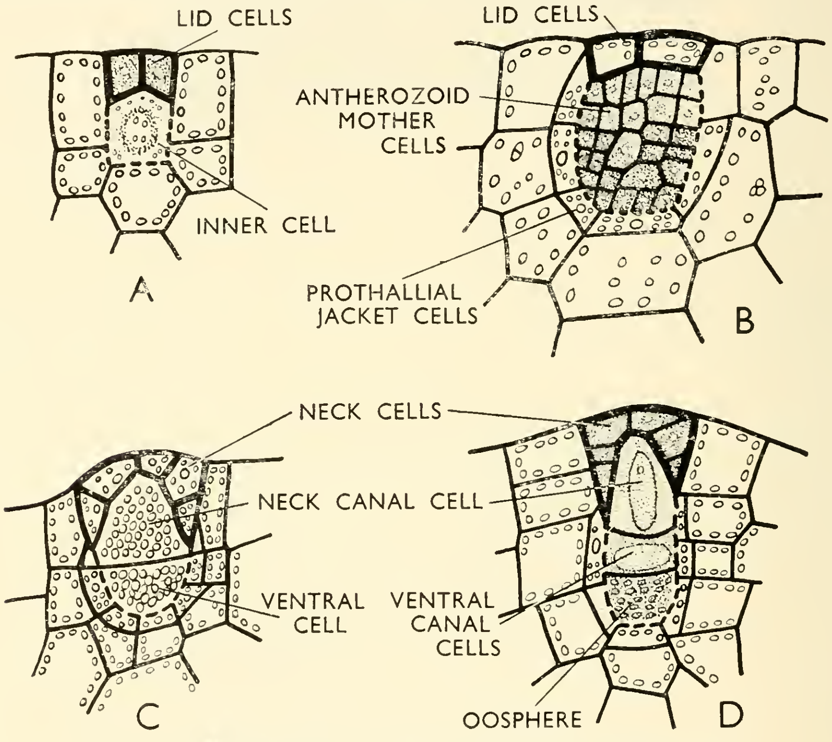

Fig. 537.—*Marattia fraxinea*. Development of reproductive organs. A and B, Antheridium. C and D, Archegonium. (*After Goebel.*)

Development of the Archegonium

The archegonium arises from one epidermal cell which divides into a row of three, as in *Dryopteris*. The middle one forms the neck canal cell (sometimes abortive), the oosphere and the ventral canal cell. The upper one forms a three-tiered neck, which scarcely rises above the surface of the prothallus. The lowest forms the base of the archegonium, and with the prothallus cells helps to form the wall of the venter.

The embryo has only a very small foot, and the stem apex turns round and penetrates the prothallus to the upper surface, where the first leaf appears as if growing from the surface of the prothallus itself (Fig. 538).

Taking *Marattia* as a type of the Eusporangiatae it is of interest to note the characters in which that group show an approach towards the Spermatophyta. These are:—

1. Massive sporangia.
2. Diarch primary root in the embryonic plant, the production of which is associated with two primary leaves or cotyledons.
3. Prolonged prothallial nutrition of the embryo in contrast to an early liberation of the embryo, as in other Pteridophyta.
4. Rotation of the embryo so that the root pole faces the archegonial apex, the position normal in Seed Plants.

We have ground, therefore, for supposing that although in some respects more primitive than the Leptosporangiatae, the Eusporangiatae stand closer to the origin of the Pteridospermae than do the former group, which is more specialized along strictly Pteridophytic lines.

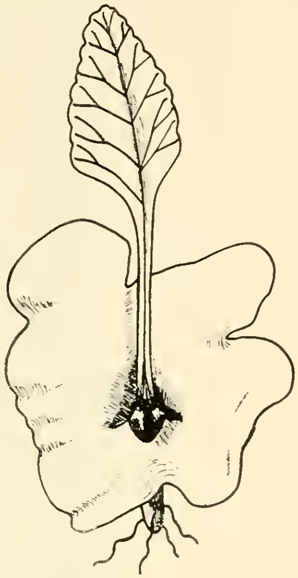

Fig. 538.—*Angiopteris teyssmanniana* (a genus closely allied to *Marattia*). Prothallus showing perforation by first leaf of developing embryo. (*After Goebel.*)

Eusporangiatae: Ophioglossaceae

In the Ophioglossaceae the stems are subterranean, the aerial portion only consisting of a single leaf which branches into a sterile lamina and a fertile spike on which the sporangia are formed marginally. The sporangia are homosporous and eusporangiate. The prothalli are subterranean and saprophytic.

Botrychium lunaria (Moonwort)

Botrychium lunaria is a rather uncommon British plant, usually found in sub-alpine pastures (Fig. 539). The stem forms a short rod, rarely branched, and usually only an inch or two long, which is found upright beneath the soil. It bears rather thick adventitious roots and is covered with old leaf bases. At its upper end arises a single leaf, 6 to 9 in. long, with a sheathing base. The single petiole bears two distinct leaf segments: one is sterile and bears a lamina which is divided on each side of the rachis into six to eight kidney-shaped pinnae with branching veins. The fertile segment, which is attached at the base of the sterile one, has no lamina and consists of a rachis bearing two ranks of pinnately arranged appendages, on each of which are two parallel rows of sporangia. Normally only one such leaf is produced each year.

FIG. 539.—*Botrychium lunaria.* Two plants showing fertile and vegetative leaf segments. About half size.

ANATOMY OF THE STEM

The stem grows from a single apical cell, which is sunk beneath a covering of successive leaf rudiments, each leaf apparently corresponding to a segment formed by the apical cell. The leaf of the current year has a completely sheathing base, which surrounds the stem apex like a tube. Inside this is the leaf for the next year, with sterile and fertile segments already formed (Fig. 540). There is no circinnate arrangement of the young leaves as in other Ferns. Two or three other leaf rudiments for future years may also be present. The basal sheath of the embryonic leaf is split into two portions, a division which remains even in the mature leaf of *B. virginianum* and suggests that this sheath is formed by the fusion of two stipules such as occur in *Marattia.* From the base of each leaf arises one adventitious root, which bores its way out through the leaf sheaths of the older leaves.

The vascular structure of a stem such as that of *Botrychium*, which is small in relation to the leaves it bears, often presents difficulties of interpretation. It is not clear, for example, how much of it is made up of the leaf traces. At the base of the young plant there is, however, a protostele, surrounded by an endodermis, and this develops at higher levels a medulla, which is sometimes mixed with isolated tracheids (Fig. 541). The leaf trace is a simple arc of vascular tissue, which leaves a considerable leaf gap in the stele. Across this gap an endodermal band is organized, independent of the primary endodermis and often stretching into the pith. It interrupts the continuity between pith and cortex through the leaf gap, though for what reason is not known.

The xylem consists of very thick-walled tracheids with the protoxylem internal, *i.e.*, endarch, and, what is highly peculiar, traces of a **cambium** and of secondary vascular tissue are found in old stems. In *B. virginianum*, mentioned above, there is quite a considerable amount of secondary thickening (Fig. 542), a unique case among present-day Ferns, though not uncommon in fossil types. We are justified, therefore, in regarding the genus *Botrychium* as primitive, with certain very ancient features of structure.

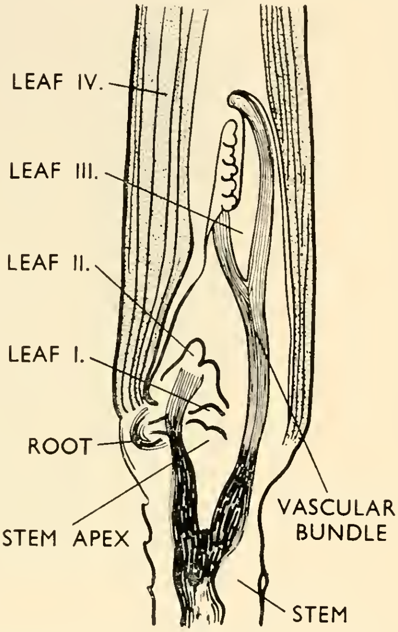

Fig. 540.—*Botrychium lunaria.* Longitudinal section of the stem apex showing successive development of leaves. (*After Goebel.*)

The *Botrychium* plant has been interpreted by some morphologists as entirely axial, with four successive dichotomies. The first is the separation of the leaf from the stem and the third is the separation of the fertile and sterile leaf segments. The second and fourth are represented only by the divisions of the vascular strand in the petiole and in the leaf segments respectively. If this view be established, then the so-called " leaf " is an axial branch and the affinity of *Botrychium* with the fossil Psilophytales is brought much closer.

Anatomy of the Root and Leaf

The root contains as a rule one simple collateral strand (Fig. 543). The simple arc of vascular tissue which forms the lower part of the leaf trace becomes a U-shaped band in the petiole. Just below the attachment of the fertile segment of the leaf the band splits laterally into two. Each of the

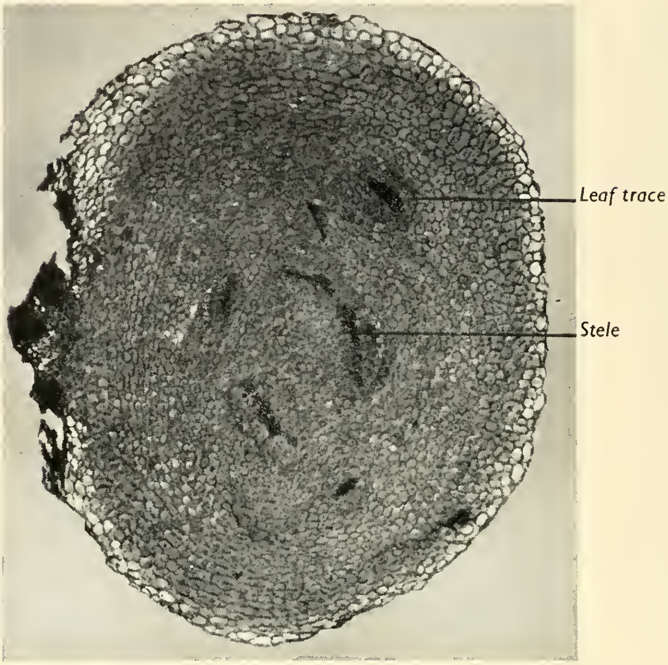

FIG. 541.—*Botrychium lunaria.* Transverse section of an old rhizome showing medullated stele.

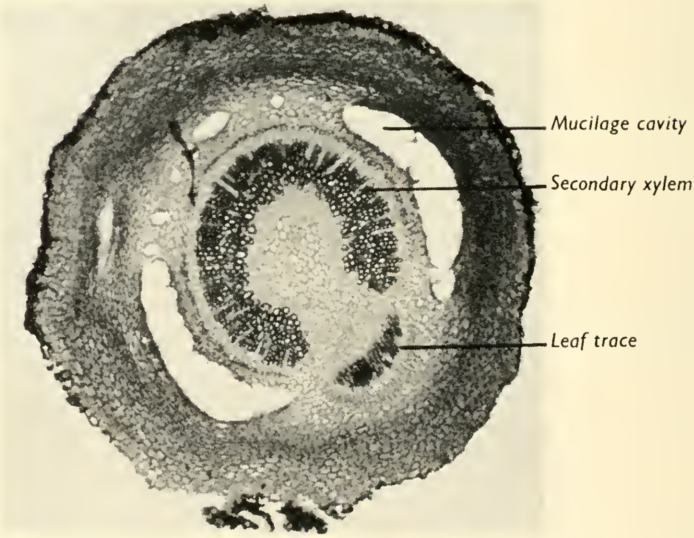

FIG. 542.—*Botrychium virginianum.* Transverse section of rhizome showing secondary thickening.

curved halves detaches a small bundle from its edge, which a little further up reunites with the inner face of the same half trace. The portion between this point of junction and the edge is then detached and passes into the rachis of the fertile segment, which therefore receives two strands (Fig. 544). This curious process is repeated in the sterile segment at the attachment of each pair of pinnae, but each pinna receives only one strand. This anatomical evidence strongly supports the view that the fertile segment represents the two basal pinnae of the leaf, fused together. Normally these alone are sporangiferous, but abnormal specimens are known in which sporangia occur also on other pinnae. Primitively the leaf was probably all fertile, but the reproductive organs have now become limited to the basal portion.

FIG. 543.—*Botrychium lunaria.* Transverse section of root.

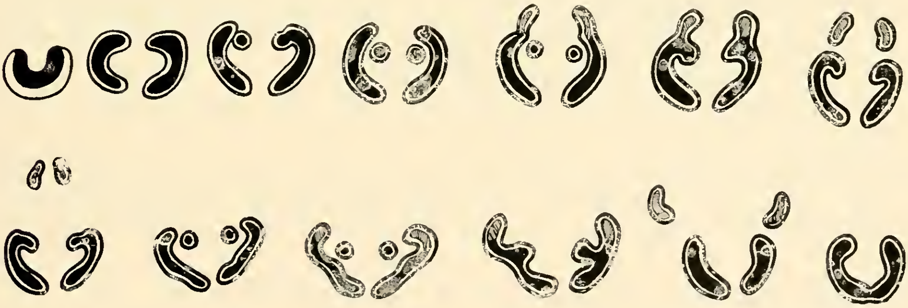

FIG. 544.—*Botrychium virginianum.* Top line of figures illustrates the origin of the double trace to the fertile leaf segment. Lower line of figures illustrates the origin of the single pinna traces in the sterile segment. (*After Chrysler.*)

THE SPORANGIUM

The sporangia are spherical and separate, with massive walls (Fig. 545). There is no annulus and dehiscence takes place between two transverse rows of specially small cells. Each sporangium produces from 1,500 to 2,000 spores (Fig. 546). The sporangia are sessile on the two margins of the rachis which bears them.

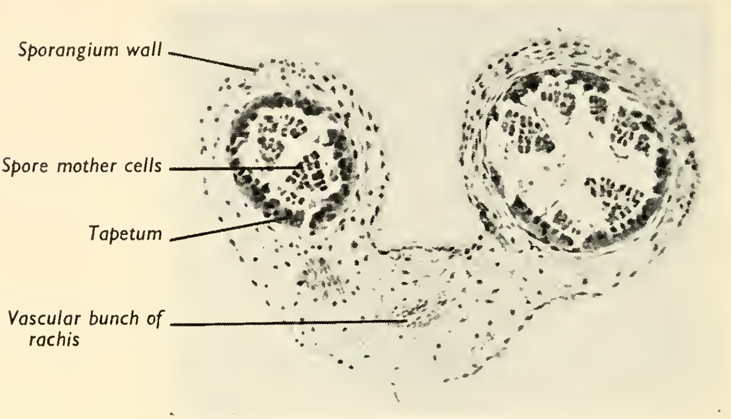

FIG. 545.—*Botrychium lunaria.* Transverse section of fertile leaf pinna passing through two of the thick-walled sporangia.

THE GAMETOPHYTE

The prothallus is very difficult to find, as it is a very small tuberous body, only a millimetre or two long, which lives saprophytically underground. It grows slowly by a group of apical cells and is wholly parenchymatous (Fig. 547). It contains a mycorrhizal Fungus which enters through the rhizoids of the prothallus and infects principally the lower parts of the tissue. Along the upper surface of the prothallus is a ridge, with antheridia (Fig. 548) on top and archegonia along its flanks. The antheridia and archegonia are very similar to those of *Marattia.* The archegonia (Fig. 549) usually mature before the antheridia, in contrast to those of the Leptosporangiate prothallus.

DEVELOPMENT OF THE EMBRYO

The embryo is at first an oval mass of undifferentiated cells. When it begins to grow out from the prothallus it forms a central strand of elongated cells which connect the primary root (outwards) to the stem apex (inwards). The innermost part of the tissue swells up, becoming the **foot,** and the stem apex is thus pushed to one side. Around the stem apex there arises a ring wall of tissue which is called the **cotyledon.** It is later broken through by the first leaf, whose base then surrounds the apical cell. We may perhaps regard this cotyledon as a leaf base of which the upper portion does not develop.

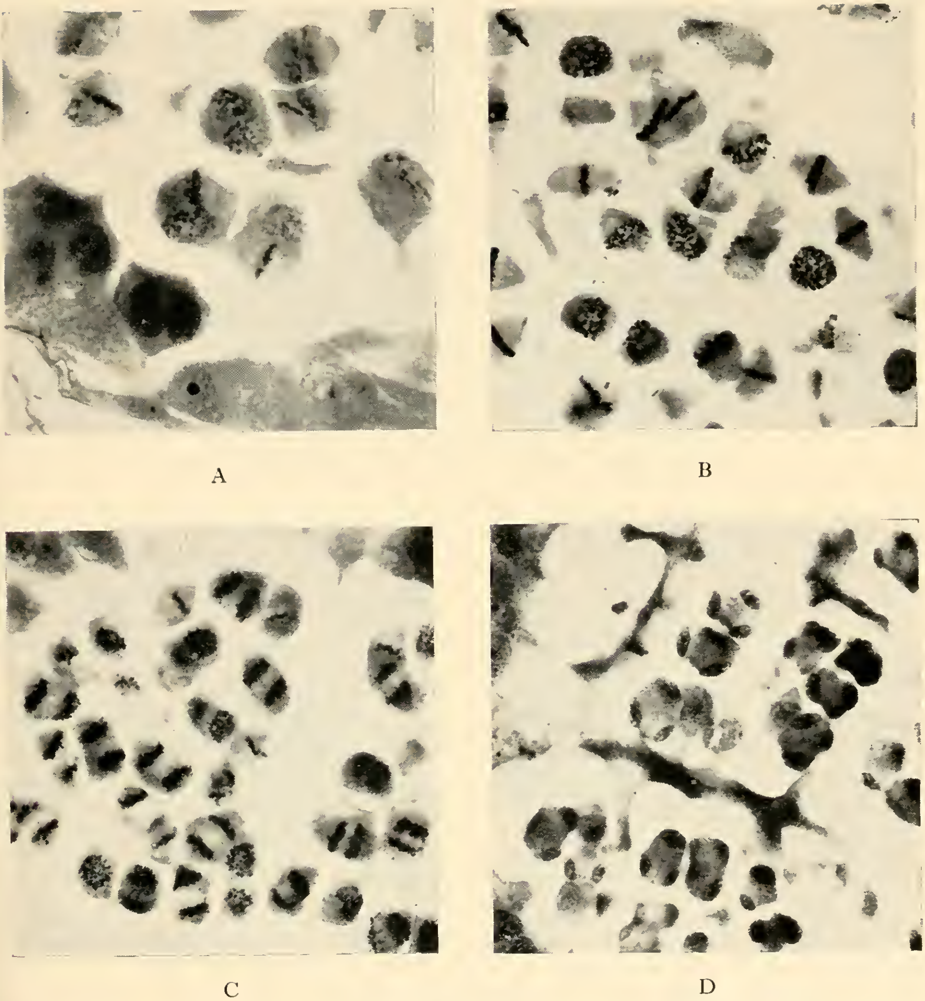

FIG. 546.—*Botrychium lunaria.* Stages in meiosis of spore mother cells. A, Heterotypic prophase. B, Heterotypic metaphase. C, Late heterotypic anaphase. D, Homotypic telophase showing formation of spore tetrads. The plasmodial ingrowths from the tapetum appear among the developing spores.

At this stage the embryo becomes free from the prothallus. It continues to produce small immature leaves and thick roots for several years, and it is not until the plant is eight to ten years old that it puts up its first green leaf. All this time it lives underground as a saprophyte, without chlorophyll, and except for the growth of the roots it hardly increases in size. This prolonged immaturity is characteristic of the small family Ophioglossaceae. This family includes besides *Botrychium* the genus *Ophioglossum*, which is of world-wide distribution, including Britain, and *Helminthostachys zeylanica*, a plant of south-eastern Asia and Australia.

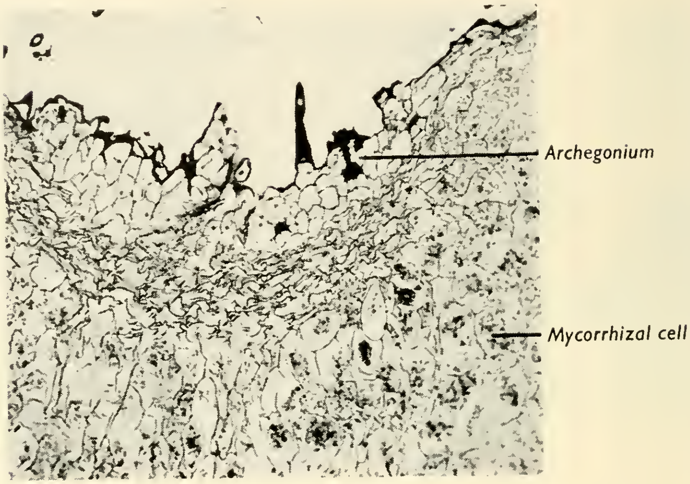

FIG. 547.—*Botrychium virginianum.* Section of a prothallus showing archegonia and mycorrhizal tissue.

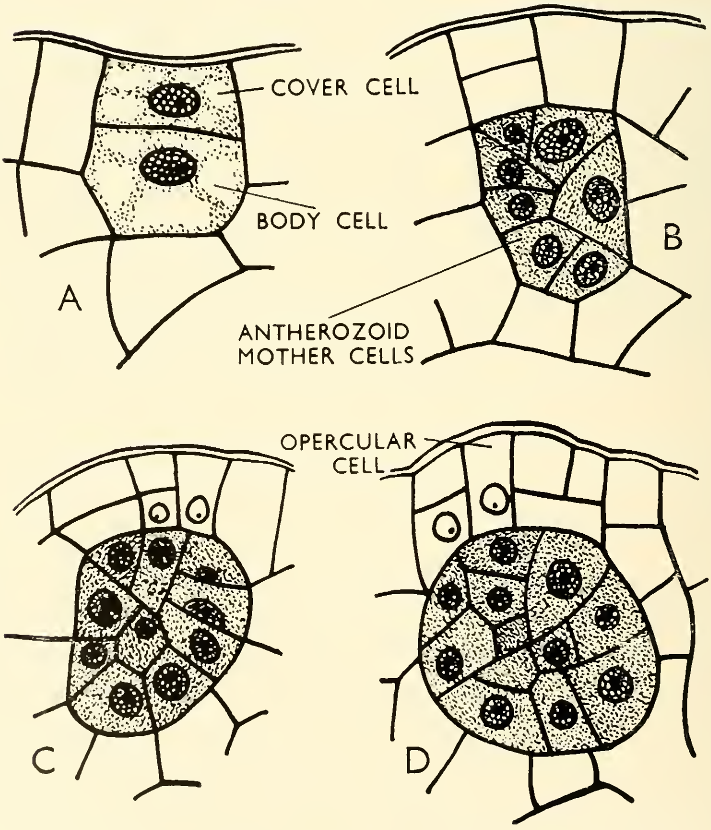

FIG. 548.—*Botrychium virginianum.* Development of the antheridium from a superficial cell of the prothallus. (*After Campbell.*)

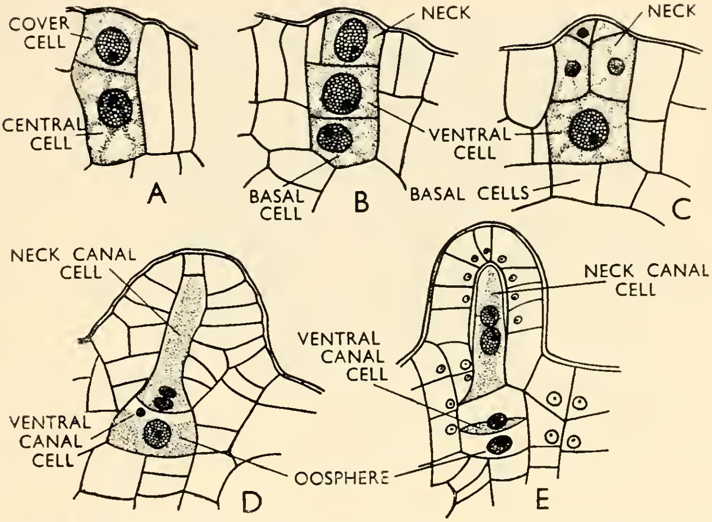

FIG. 549.—*Botrychium virginianum.* Development of the archegonium from a superficial cell of the prothallus. (A *to* D *after Campbell,* E *after Jeffrey.*)

Hydropterideae: Salviniaceae

The Salviniaceae are small floating plants which are often referred to as the "Water Ferns." They stand apart from all the other Filicales in being **heterosporous**, forming **microspores** which produce male prothalli and **megaspores** which produce female prothalli, both being enclosed within the spore walls. Both types of spores are found in separate sori, which are each covered by a closed indusium, forming a **sporocarp.**

Azolla filiculoides

Azolla is a very small leafy plant, floating freely on the water surface (Fig. 550). There are only three species, all tropical or sub-tropical. Our type is native to America. Another species, *A. caroliniana*, is often distinguished from it, but the differences are not constant. About seventy years ago it arrived in southern Europe, from whence it has spread northwards and is now found in many parts of Britain. It is easily recognizable, covering ponds and ditches, and having a striking crimson colour and a feathery appearance.

The delicate stems bear alternating leaves in two rows on the upper surface. Each leaf is divided into two unequal parts. The upper lobes are somewhat smaller and overlap closely along the stem. They have a well-marked **palisade tissue** on their upper (abaxial) surfaces, but have stomata on both surfaces (Fig. 551). An aperture on the lower (adaxial) surface opens into a slime-filled cavity in the leaf tissue (Fig. 552), in which lives, possibly symbiotically, a Blue-green Alga, *Anabaena azollae*, which is credited with the power of Nitrogen fixation. These upper lobes contain chlorophyll

FIG. 550.—*Azolla filiculoides.* Floating frond with roots. Twice natural size.

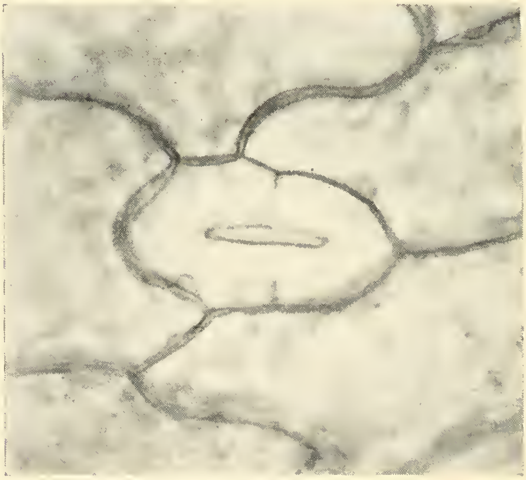

FIG. 551.—*Azolla filiculoides.* Superficial view of leaf showing a stoma. Note that the pore is transversely elongated with respect to the guard cells, the wall between which is in process of breaking down.

and are obviously photosynthetic organs. The upper surface is velvety with epidermal papillae and is unwettable, which is naturally advantageous in preventing the blockage of the stomata with water.

The lower lobes are somewhat broader than the upper and consist as a rule of only one cell layer. They are very poor in chlorophyll, and it has been shown that they absorb water freely, their surface being wettable. The

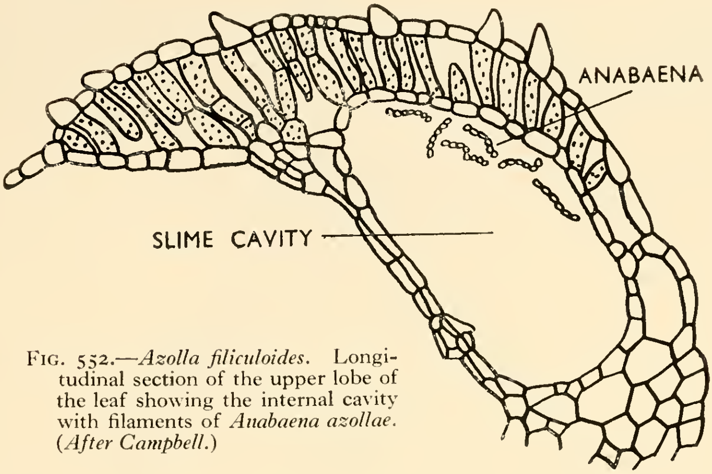

Fig. 552.—*Azolla filiculoides.* Longitudinal section of the upper lobe of the leaf showing the internal cavity with filaments of *Anabaena azollae.* (*After Campbell.*)

close overlapping of upper and lower lobes not only protects the growing points but also serves to entrap air bubbles, which give the plant its buoyancy.

From the under side of the floating stems arise the small adventitious roots, which hang down in the water. The primary root alone bears root hairs.

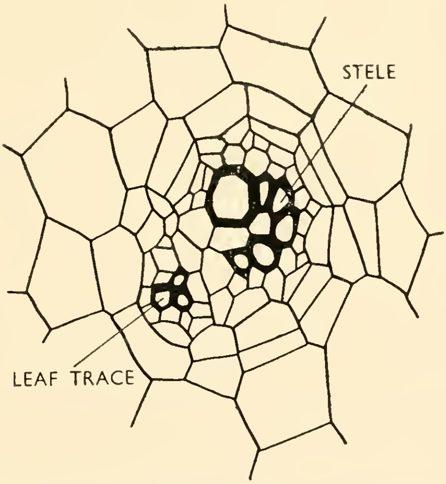

Fig. 553.—*Azolla filiculoides.* Transverse section of the stem stele showing reduced siphonostelic structure with leaf trace and leaf gap. (*After Eames.*)

Anatomy of the Axis

The stem of *Azolla* grows by means of a wedge-shaped apical cell, which cuts off two rows of segments. A leaf arises from each segment thus formed. The vascular structure of the stem is very much reduced, as in other aquatic plants (Fig. 553). It consists of a very small central stele containing a few spiral tracheids and phloem cells arranged around a very minute pith. In spite of its reduction it is therefore essentially a **siphonostele** and there are distinct, though minute, leaf gaps where the leaf traces are inserted. This simple stele is surrounded by a pericycle and an endodermis the brown-coloured walls of which appear to be suberized. There is a rather loose cortex with no distinct epidermis and no cuticle.

The root structure is similar, but still smaller (Fig. 554). The root cortex consists principally of a single row of very large cells. The root hairs are arranged in short, transverse rows, alternating at intervals on two sides of the root. A final crop of root hairs is produced underneath the root cap, which then drops off, leaving the apical mass of root hairs exposed.

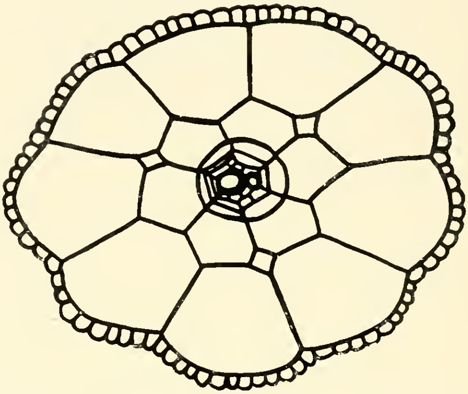

Fig. 554.—*Azolla filiculoides.* Transverse section of root showing outer and inner cortical layers and well-marked endodermis. (*After Queva.*)

The Sporangia

On the side branches of the stem are produced the fertile leaves or **sporophylls,** which are always the lowest leaves on the branch. Their structure is complex, but it has been explained by von Goebel as follows: The sporophyll, like the vegetative leaf, consists of two lobes. The lower lobe divides very early into two portions, at the apices of which arise the sori. The indusium grows out as a ring-wall below the sorus and encloses it completely except for a micropyle-like opening at the top, resembling very much an integument round the ovule of a Seed Plant. The upper lobe of the sporophyll has the form and structure of the corresponding lobe in an ordinary leaf, including the *Anabaena* cavity, but its margins are produced into wings which partly enclose the sori.

The sori are of two kinds: **microsori** and **megasori,** so called according to whether they contain **microsporangia** or **megasporangia.** Although the sori are " unisexual " they have been reduced from a hermaphrodite condition, which they still retain in their early development. In both cases development begins with the formation of a megasporangium at the tip of the placenta and microsporangia round its base (Fig. 555). In a megasorus the megasporangium contains thirty-two potential megaspores, but all except one abort, as well as the microsporangia. In a microsorus all the megaspores abort and the microsporangia continue development. The result is that a megasorus contains a single megasporangium with a single megaspore, and a microsorus contains numerous long-stalked microsporangia, containing sixty-four microspores * (Figs. 556 and 557).

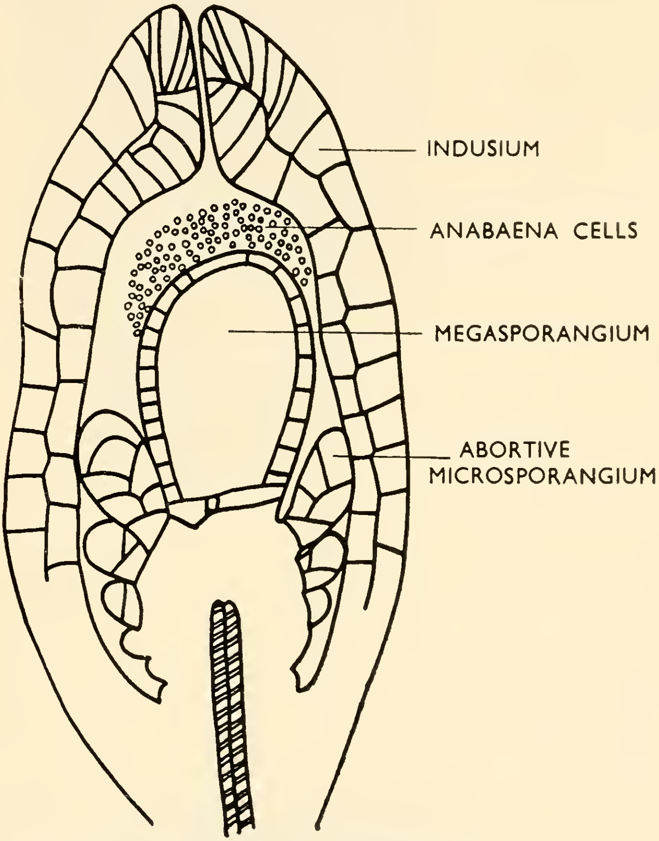

Fig. 555.—*Azolla filiculoides.* Longitudinal section of a developing megasorus showing abortive microsporangia. (*After Goebel.*)

Development of the Microsporangium

The developments inside the sporangia are highly peculiar. Let us take the microsporangium first. Sixty-four spores are formed, surrounded by a nutritive wall of cells, the **tapetum,** which forms the inner layers of the

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* In some species the sporangium is completely encircled by an oblique ring of cells which probably represents a vestigial annulus.

sporangial wall. The cells of the tapetum disorganize and a nucleated mass of protoplasm results, which envelops the spores. The spores move to the periphery, and the tapetal plasmodium develops a number of vacuoles in which the spores are grouped in approximately equal numbers. Then each

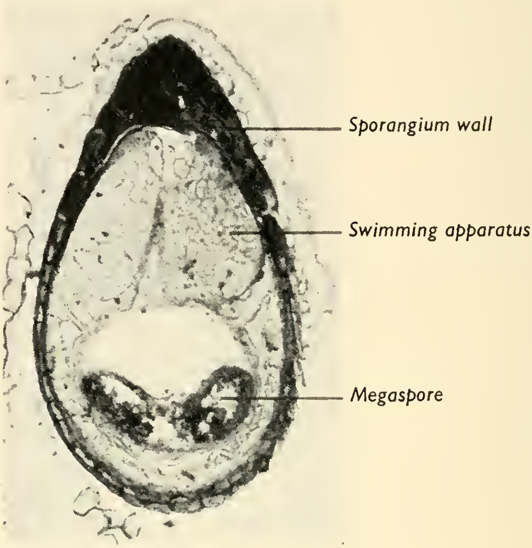

FIG. 556.—*Azolla filiculoides*. Longitudinal section of a megasporangium. The megaspore wall is somewhat collapsed.

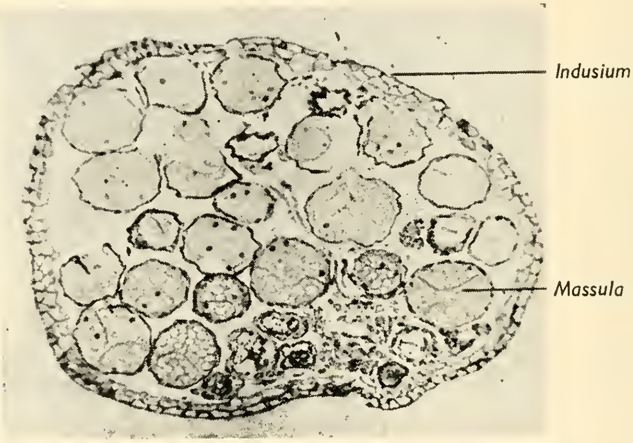

FIG. 557.—*Azolla filiculoides*. Transverse section of a microsorus with a large number of microsporangia containing massulae.

vacuole becomes divided by partitions into a number of **alveoli.** Each group of spores thus enmeshed in the alveoli is called a **massula** (Fig. 558). From the wall of the enclosing vacuole there grow out a number of radial processes, like hairs, which end in barbed hooks. These extraordinary structures, formed from a vacuole membrane, are called **glochidia,** and they function by attaching the liberated massulae to the megaspore.

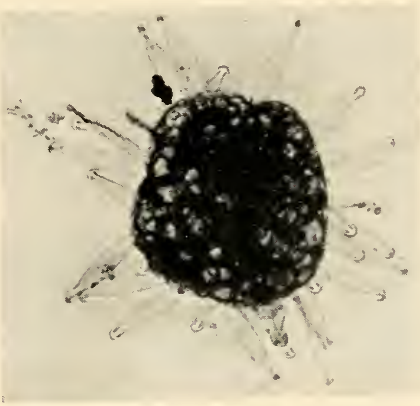

Fig. 558.—*Azolla filiculoides.* Massula after liberation showing hooked glochidia and alveoli containing microspores.

Development of the Megasporangium

In the megasporangium the lower part of the sporangial wall first of all disintegrates, leaving the single large megaspore at the bottom of the sorus covered only by the indusium. The tapetum then forms a plasmodium, as in the microsporangium, which divides into four massulae. One of these envelops the megaspore, forming a sculptured **epispore,** marked by cavities and projecting processes. The other three massulae are grouped above the megaspore. They become highly vacuolated and harden into spongy bodies called collectively the **swimming apparatus** (Fig. 559).

Inside the indusium, above the megaspore, there are present numerous spores of *Anabaena.* These are shed along with the megaspore and germinate with it so that the association of the two plants is kept up from one generation to the next.

The indusium partly disintegrates, liberating the megaspore and its appendages, but the upper portion and the remnants of the sporangial wall remain attached to it, forming a kind of umbrella. The microspore massulae are similarly liberated and the glochidia hook themselves to the sculpturing of the epispore round the megaspore, thus ensuring the proximity of the prothalli.

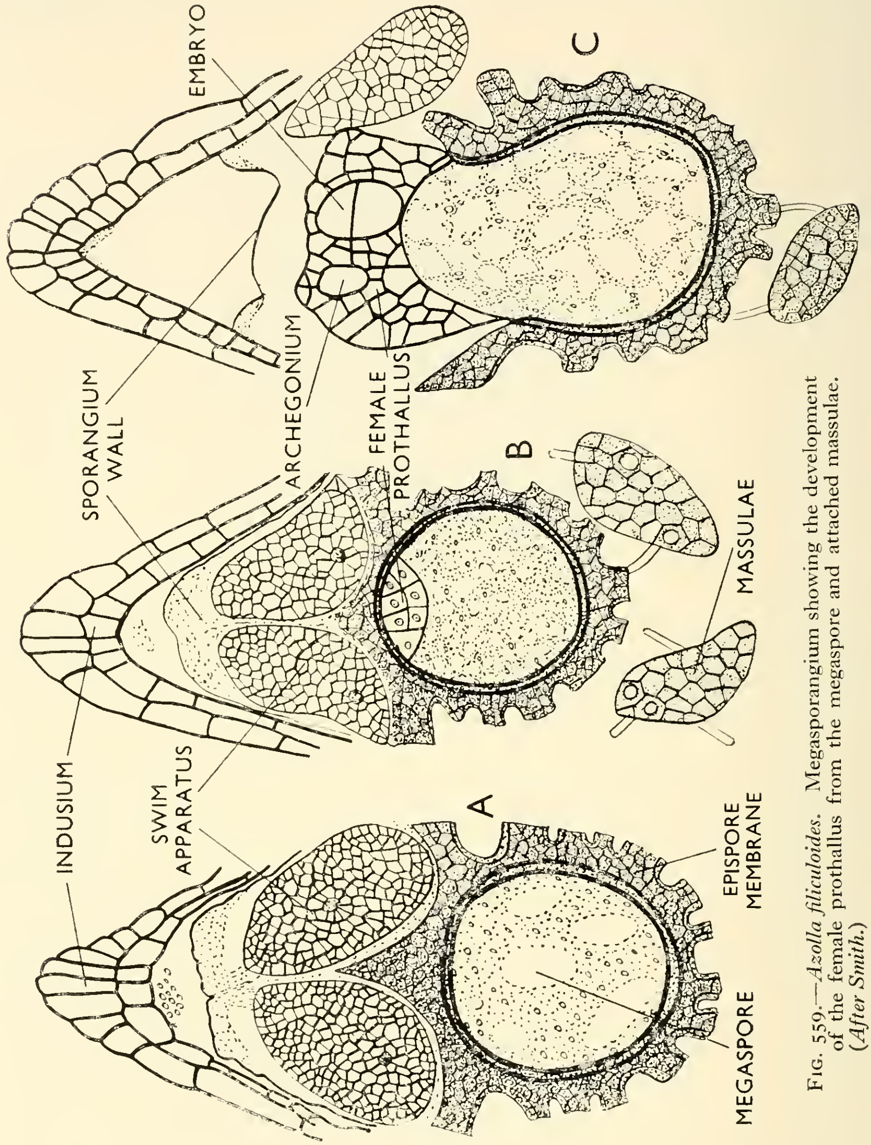

FIG. 559.—*Azolla filiculoides.* Megasporangium showing the development of the female prothallus from the megaspore and attached massulae. (*After Smith.*)

STRUCTURE OF THE GAMETOPHYTES.

The megaspore opens at the top and exposes a small, pale-green **female prothallus,** which remains attached to the megaspore wall (Fig. 559). This small mass of cells at first develops only one archegonium, and only if this is unfertilized are more formed. Owing to the efficiency of the massula arrangement, however, fertilization is usually promptly ensured.

The archegonia are of a simple type, immersed in the prothallus, with a four-tiered neck which projects slightly. The venter has no wall (Fig. 561).

Inside the megaspore a considerable amount of nucleated protoplasm remains, filling the cavity below the prothallus (compare *Selaginella*, p. 587). It is finely granular and apparently contains food reserves.

As the megaspore opens by a three-rayed slit the prothallus has a correspondingly triangular outline in transverse section.

The microspores, after being liberated in massulae by the decay of the sporangial walls, form extremely reduced **male prothalli** (Fig. 560). The spore wall splits by a three-rayed slit and part of the contents bulge out and are cut off from the rest of the spore contents by a wall. The cell so formed becomes the antheridium. The rest of the spore contents represent the vegetative part of the male prothallus, which consists of two cells, as a second small cell is cut off inside the spore. The antheridial cell undergoes further divisions, cutting off a cover cell and wall cells, enclosing a central cell, which divides to form eight antherozoid mother cells.

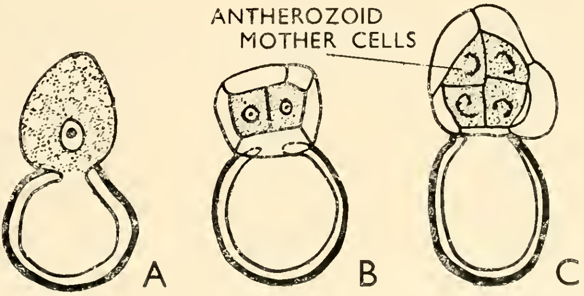

Fig. 560.—*Azolla filiculoides*. Development of the male prothallus, which consists of a single antheridium. (*After Smith*.)

The whole male prothallus is formed embedded in the substance of the massula, and the antherozoids, which are of the Fern type, make their way out through it.

Neither male nor female prothallus ever becomes free from the spore and has no independent life. They are nourished entirely by the reserves in the spores themselves, and consequently are only short-lived.

The Embryo

The early development of the embryo resembles that in the Leptosporangiatae. The basal part of the embryo remains embedded in the prothallus as a **foot,** the primary root being more or less lateral (Fig. 562). The first leaf envelops the apex like a funnel and is called the **cotyledon.** Large intercellular spaces develop in it, and the whole embryo plant, often carrying with it the megaspore still attached to the foot, floats to the surface, where growth commences.

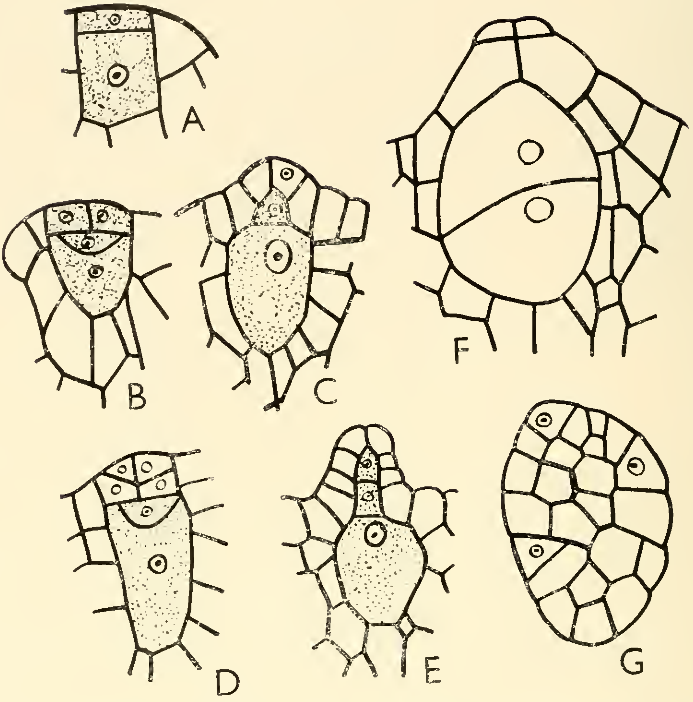

Fig. 561.—*Azolla filiculoides.* A to E, Stages in the development of the archegonium. F, Two-celled embryo. G, Young embryo. (*After Smith.*)

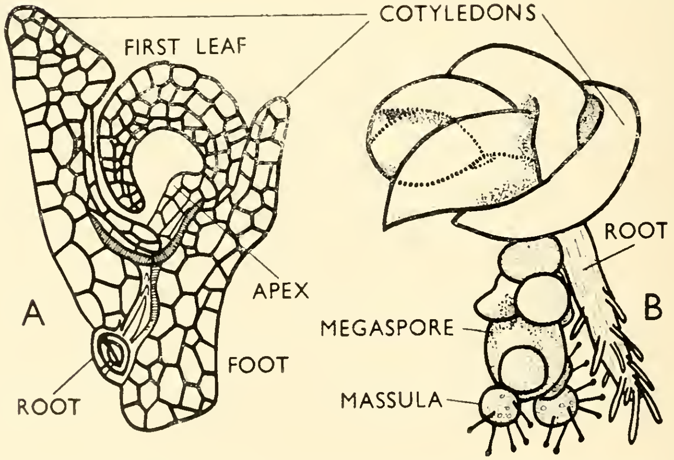

Fig. 562.—*Azolla filiculoides.* A, Longitudinal section through a mature embryo. B, Embryonic plant still attached to the megaspore. (*After Eames.*)

Isolated though *Azolla* appears in its peculiar structure, there are certain points of resemblance to the Hymenophyllaceae, also a somewhat reduced group. The basipetal order of development of the sporangia on the placenta and the sheathing indusium have their parallels in this latter group, and it seems probable that these are the nearest relatives to our present type among the true homosporous Ferns.

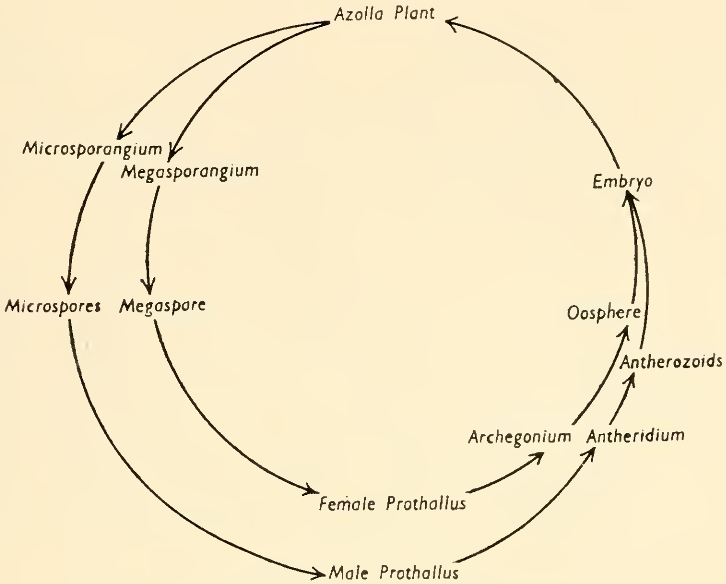

FIG. 563.—Life-cycle of *Azolla filiculoides*.

EVOLUTION OF THE STELAR ANATOMY IN THE FILICALES

The examples of the Filicales which we have described exhibit a complex stelar anatomy in the structure of the stems, and in order that this may be clearly understood it is desirable to say something about the way in which it probably evolved (Fig. 564). We can gain information about this problem from three sources. One is the comparative study of different present-day types of Ferns, another is the comparison of living with fossil genera, and a third is the study of development in living forms.

The simplest kind of stele is the **protostele** (Figs. 565 and 566). It consists of a central solid mass of xylem surrounded by a ring of phloem and bounded on the outside by a pericycle. Such a stele may be found in *Gleichenia* and *Lygodium* among present-day forms, and in *Botryopteris* and its allies among the earliest fossil Ferns. In such types the leaf trace is also simple and consists of a single vascular strand which splits off from the protostele and comprises a mass of xylem on the side towards the stem and phloem towards the outside. This leaf trace is completely surrounded by an endodermis and causes no break in the central xylem core.

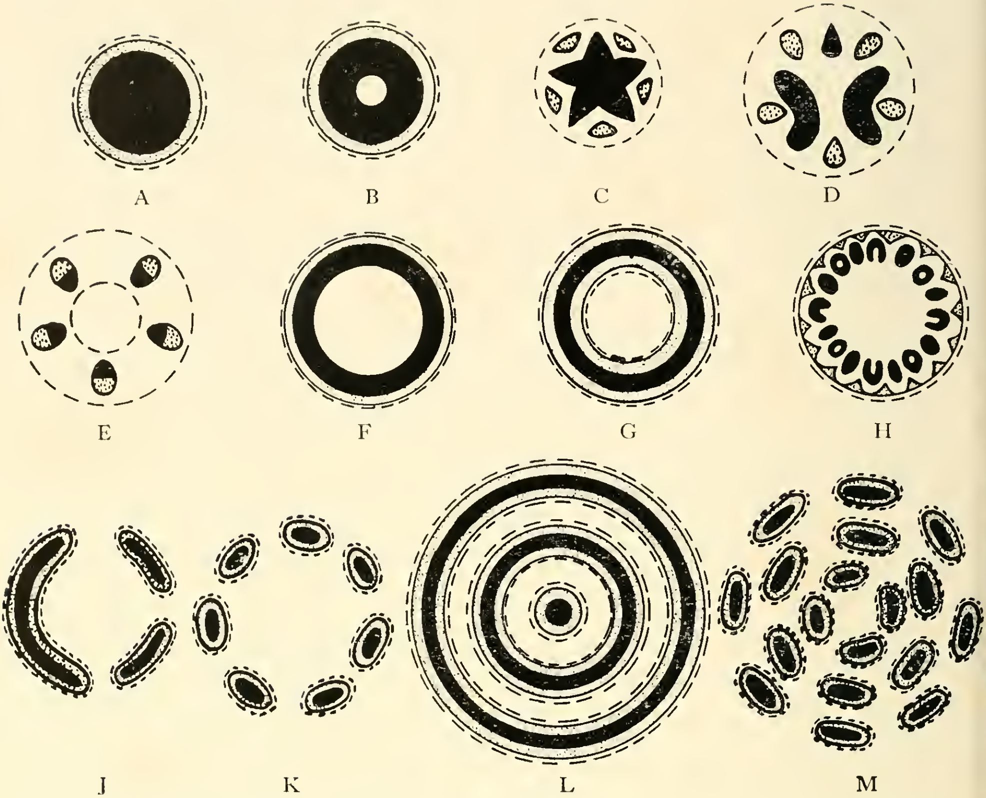

FIG. 564.—Types of stelar structure. A, Typical protostele. B, Medullated protostele. C, Actinostele. D, *Lycopodium* type. E, *Equisetum* type. F, Ectophloic siphonostele. G, Typical amphiphloic solenostele. H, *Osmunda* type. J, Typical dictyostele. K, Perforated dictyostele. L, Polycyclic solenostele. M, *Marattia* type. (*After Ogura.*)

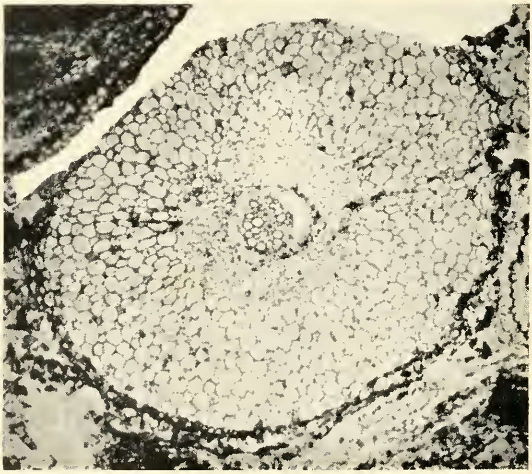

FIG. 565.—*Botryopteris cylindrica*. Transverse section of stem showing protostele.

Starting from this simple condition, it has been necessary, especially in larger plants, to increase the area of the stele.

One way of doing this is by the extension of the xylem mass radially outwards into a series of wings or flanges, with the protoxylems at the extremities. This is called an **actinostele** (Fig. 564, C). It is characteristic of many of the early fossil Pteridophyta and survives in some species of *Lycopodium* and *Psilotum*.

Another method has been to increase the diameter of the stele by the admixture of parenchymatous cells with the tracheids (Fig. 567), which later results in the central part of the xylem, becoming entirely replaced by a parenchymatous **medulla** or **pith**.

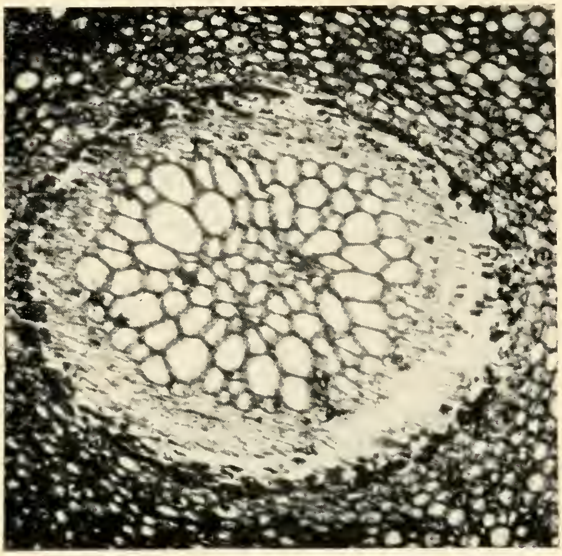

FIG. 566.—*Botryopteris cylindrica.* Protostele enlarged showing mesarch protoxylems and surrounding phloem zone.

In this way the solid protostele is converted into a tubular structure with a central medulla, the **siphonostele**. The first condition is illustrated by the fossil type, *Metaclepsydropsis duplex*, in which the inner zone of the stele consists of a mixture of tracheids and parenchyma, that is to say, a " mixed pith." This type may therefore be regarded as intermediate between a true protostele and a stele with a completely parenchymatous pith. Fossil members of the Osmundaceae also illustrate the complete transition to a medullated stele (Fig. 568). *Botrychium* also illustrates a type in which the pith has developed within the stelar tissues. The next stage is the development of an endodermis between the tubular stele and the pith, forming what is termed a **solenostele** (Fig. 564, G).

Very soon after the evolution of this type of stele we find that the leaf trace becomes more elaborate, and instead of merely separating off a small

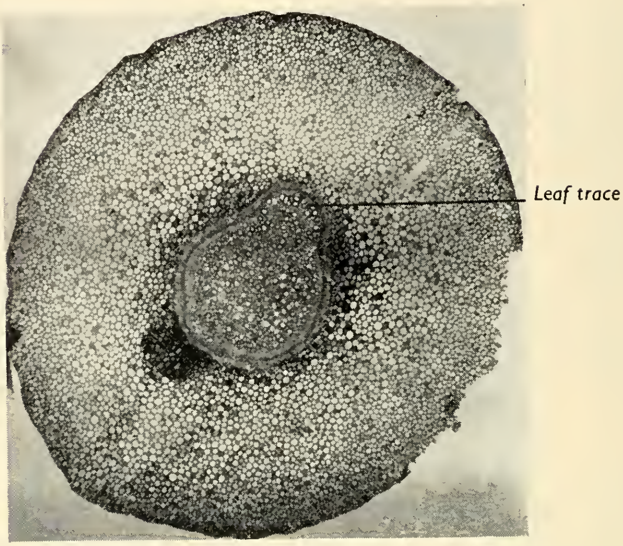

FIG. 567.—*Gleichenia flabellata.* Transverse section of stem showing leaf trace leaving protostele in which parenchyma cells are mixed with the tracheids.

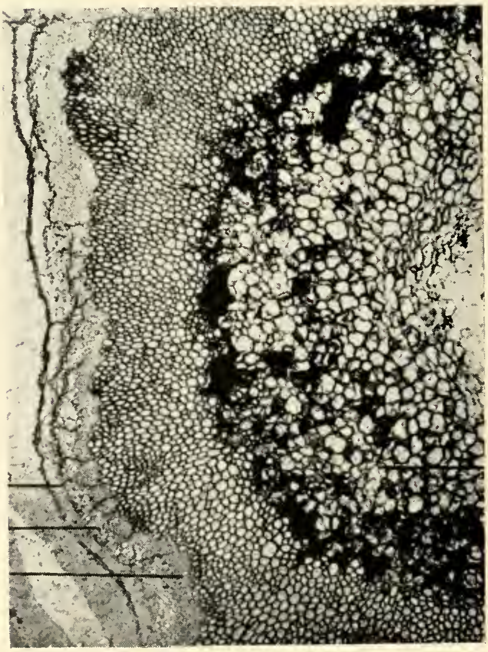

FIG. 568.—*Thamnopteris schlechtendalii.* Transverse section of stem showing medullated protostele.

segment of the stele, it breaks right through the ring, forming a gap above the point where the trace is given off. Through these gaps pith and cortex become continuous, and the gaps may become lined not only with phloem but also by the pericycle and endodermis. As an example of this we may cite the case of *Loxsoma cunninghamii*.

In relation to the leaf gaps we find that in some examples the phloem and pericycle spread round the xylem, so that the original xylem ring is bounded both inside and outside by successive layers of phloem, pericycle and endodermis. Such a condition is termed an **amphiphloic solenostele.** We see examples of this in *Dennstaedtia* and *Dicksonia* (Figs. 569 and 570) among the present-day genera, and also in *Alsophila*, though in this genus the solenostele soon becomes split up into a more complex form of dictyostele such as is referred to below.

In such a type of stelar anatomy the central tissue is isolated from the cortex by a continuous layer of endodermal cells, except in the leaf gaps at the nodes. Where the stem is short and the leaves are set closely together the leaf gaps overlap, so that several appear in a section taken at any level. Thus the tubular stele is reduced to a network, as in *Dryopteris*, and this is called a **dictyostele** (Fig. 564, J). A further step is the formation of openings, or **perforations,** which produce a dictyostelic condition even where the leaves are separated by long internodes, as in *Pteridium*. The stele of such Ferns consists of a circular column of vascular tissue resembling a tube of wire netting, the holes in the network being formed partly by the perforations in the vascular tissue of the stele and partly by the leaf gaps. This form of the stele is obviously much more favourable to physiological interchanges between the tissues than is the continuous solenostelic tube. It may be regarded as a means of increasing the total surface of the vascular tissue, analogous to the subdivision of the leaf into filaments in submerged water plants (Fig. 564, K).

Like the stele, the leaf trace has a history of progressive elaboration. In the most ancient types it is a simple mesarch strand of xylem and phloem, with an endodermis. This very early became a flattened band, which adopted a curved outline, like a U, the opening being towards the axis, that is, to the upper side of the petiole. Mechanically such a form is favourable to rigidity, and it became the fundamental Fern type of leaf trace. In solenostelic Ferns it usually remains a single band, but in dictyostelic Ferns it is divided into meristeles, sometimes arranged in a simple U-form, sometimes, as in *Pteridium* and the larger Ferns generally, arranged in a complex pattern of many meristeles, which can only with difficulty be related to the fundamental horseshoe type (Fig. 571).

It has been stated by one authority (Sinnott) that the leaf trace in the Pteridophyta appears to have followed a course of evolution which was independent of the evolution of the stem stele and has had little influence upon it.

The final elaboration of the stelar anatomy in the Filicales consists in the development of a number of separate steles one inside the other, a condition

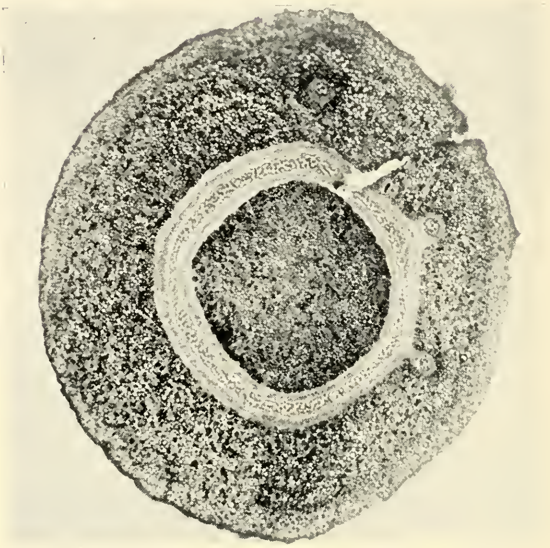

FIG. 569.—*Dennstaedtia apiifolia.* Amphiphloic solenostele showing origin of root traces.

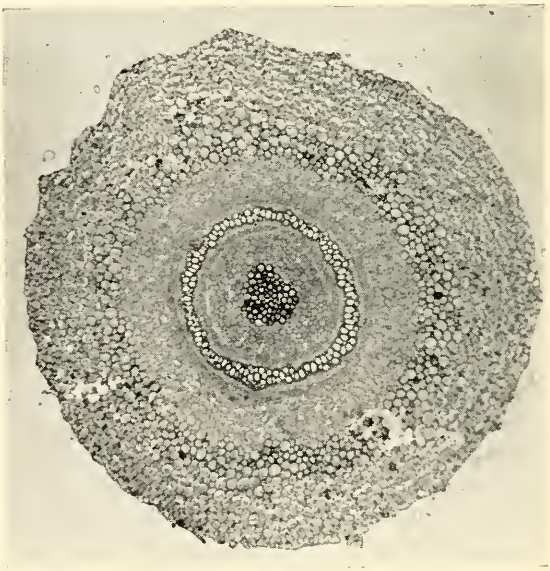

FIG. 570.—*Dicksonia punctilobula.* Amphiphloic solenostele.

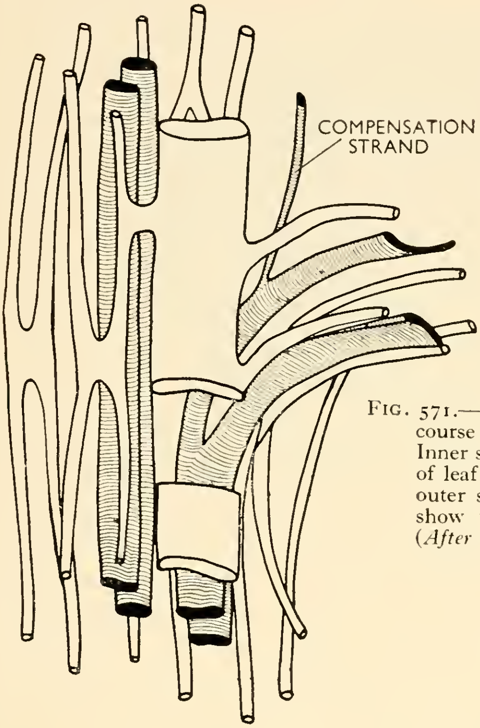

Fig. 571.—*Pteridium aquilinum.* Diagram of the course of the vascular strands at a node. Inner strands of rhizome and marginal lobes of leaf trace shaded. A piece of the dorsal outer strand of the rhizome is removed to show the branching of the inner strand. (*After Tansley and Lulham.*)

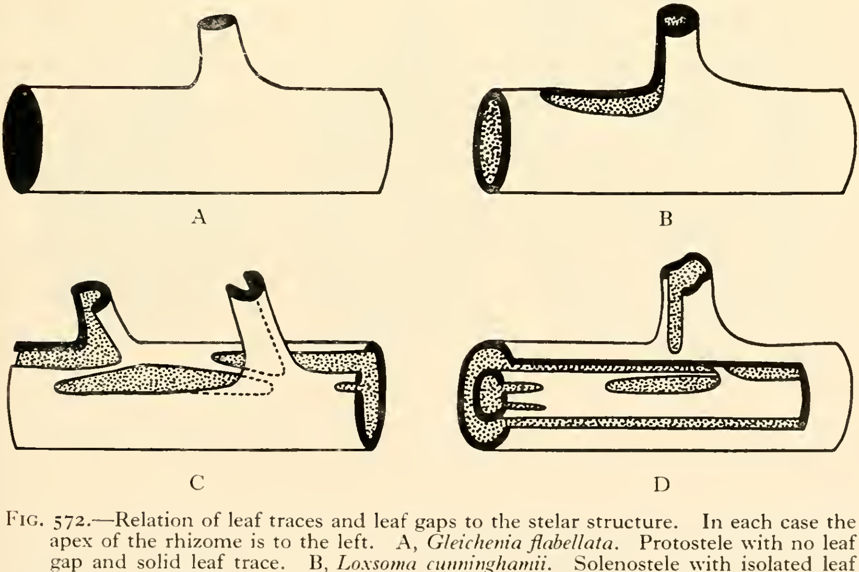

Fig. 572.—Relation of leaf traces and leaf gaps to the stelar structure. In each case the apex of the rhizome is to the left. A, *Gleichenia flabellata.* Protostele with no leaf gap and solid leaf trace. B, *Loxsoma cunninghamii.* Solenostele with isolated leaf gap and C-shaped leaf trace. C, *Pellaea rotundifolia.* Solenostele showing departure of two overlapping leaf traces. D, *Pteris elata* var. *karsteniana.* Polycyclic solenostele with part of outer stele removed to show leaf gap and compensation strand in inner stele. (*After Gwynne Vaughan.*)

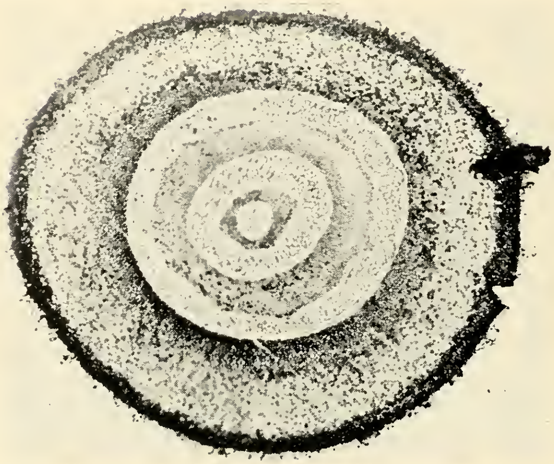

FIG. 573.—*Matonia pectinata.* Transverse section of the stem showing three concentric steles.

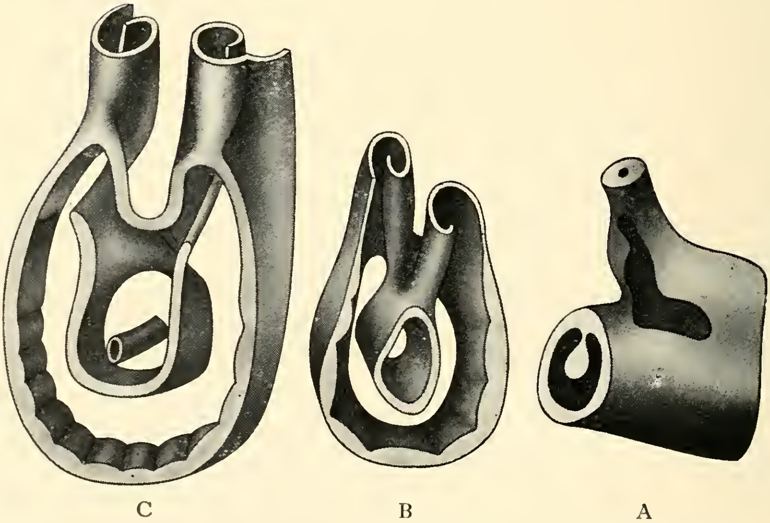

FIG. 574.—*Matonia pectinata.* Polycyclic solenostele. Drawings from wax models of the stelar system at the node. A, B and C represent different stages in maturity of the structure. (*After Tansley and Lulham.*)

which is termed **polycyclic.** Thus, as we have seen in *Pteridium aquilinum*, we have two steles, the inner one of which may be regarded as a solenostele, and the outer one as a dictyostele (Fig. 572). Since, however, leaf gaps are found in both steles and both contribute to the leaf trace, a transverse section through the stem shows two concentric rings of meristeles. In *Matonia pectinata* there are three solenosteles, but the central one, which is quite small, and may sometimes be protostelic, plays no part in the formation of the leaf trace (Figs. 573 and 574). In *Pteris podophylla* even four steles have been observed.

It is worth pointing out that the historical sequence of stages in the stelar evolution of the Fern is often passed through during the development of the individual ("Recapitulation") (Fig. 575). Thus even the highly complex polycyclic dictyostele of *Marattia* begins in the sporeling plant as a protostele, and passes through a brief solenostelic phase, firstly to a monocyclic, and finally to a polycyclic dictyostele (Fig. 564, M).

Experiments in which the leaves of various Ferns were progressively removed during development of the plant have shown the interesting fact that under these circumstances the ontogenetic sequence is reversed, the dictyostele becoming reduced to an uninterrupted solenostele and then to a protostele, while in extreme cases the vascular system at the apex may disappear altogether.

Finally it should be noted that dictyostely is essentially different from **polystely,** such as is found in some species of *Selaginella*, where two or more parallel steles lie side by side in the stem and are unconnected with each other except at points where the stem branches (see p. 580).

Fig. 575.—*Gleichenia pectinata.* Longitudinal plan of stelar construction showing change from a true protostele in the young plant through a medullated protostele to an amphiphloic solenostele in the mature plant. (*After McLean Thompson.*)

CHAPTER XV

THE PTERIDOPHYTA: LYCOPODIALES, ISOETALES, PSILOTALES AND EQUISETALES. THE CLUB MOSSES AND HORSETAILS

LYCOPSIDA

This series of the Pteridophyta was distinguished by Jeffrey on the grounds of the prevalence of small leaves, which have almost invariably a single leaf-trace bundle, without branches. These traces leave no leaf gap in the stele of the stem. They are described as **microphyllous**, partly on the above grounds and partly because the leaf is subordinate to the axis in the architecture of the shoots.

It was pointed out, when speaking of the Pteropsida, that the morphological differences of the two series are not absolute, but that in spite of exceptions their general characteristics do mark them as distinct. We might add that the prevalent tendency to form reduced or saprophytic gametophytes is another mark of distinction in the Lycopsida.

The shoot of the Lycopsida often shows a tendency to be flattened by the formation of side shoots all in one plane. The trace bundles which supply these shoots leave a gap in the stele of the main axis which is similar to the gap left by the megaphyllous leaves of Ferns. It has been repeatedly suggested that the Fern megaphyll is homologous with one of these flattened shoots in the Lycopsida and that it is therefore really a **cladode** (see p. 924) or branch structure. From this point of view megaphylls and microphylls must be regarded as two quite different types of organs, and if this be accepted the distinction between the two series is made even more emphatic. Jeffrey used the term **cladosiphonic** for the Lycopsidan type with only branch-gaps in the stele, and **phyllosiphonic** for the Pteropsidan type with leaf-gaps.

The Lycopsida include two orders, of which we shall describe the following examples :—

Lycopodiales

Lycopodiaceae (Homosporous), *e.g.*, *Lycopodium.*
Selaginellaceae (Heterosporous), *e.g.*, *Selaginella.*

Isoetales

Isoetaceae (Heterosporous), *e.g.*, *Isoetes.*

Lycopodiales

The Lycopodiales are distinguished from the Filicales by the small size of the leaves and by the fact that the sporangia are aggregated together into **cones** or **strobili,** which bear specialized leaves, on the upper surface of which the sporangia develop. These sporangia may be homosporous or heterosporous, and it is on this point that the two important families, the Lycopodiaceae and the Selaginellaceae, are distinguished; the latter are heterosporous.

Associated with the small leaves we find that the vascular anatomy is simple compared with that of the Ferns, though several steles may occur in the stem.

The development of a special structure, the **ligule,** which appears at the base of the vegetative leaves and also, associated with the sporangia, at the base of the leaves of the cones, is a further point which distinguishes the Selaginellaceae from the Lycopodiaceae. This feature is found very commonly among fossil members of the order, both those which are homosporous and those which are heterosporous. This ligule is a minute scale which arises from a superficial cell of the epidermis of the leaf base.

The living Lycopodiales are the representatives of a group which, during the Carboniferous period, formed the chief vegetation. Many of the types then growing, such as *Lepidodendron*, were large trees comparable in size with the Pines and Firs of the present time. The modern representatives are all quite small plants, seldom reaching more than a foot in height, though some of the trailing species may become longer.

They occur chiefly in peaty soils, often, in Europe, on the sides of mountains, but in warmer countries large species grow as hanging epiphytes on the trunks of trees and form part of the forest undergrowth.

We shall consider two examples of this order, *Lycopodium clavatum* and *Selaginella kraussiana*.

Lycopodium clavatum (The Club Moss)

Five species of *Lycopodium* occur in Britain, and are found most commonly on heaths and moors, chiefly in hilly districts, though they are never very common except in a few localities, where large patches of plants may sometimes be found (Fig. 576).

Lycopodium clavatum consists of an extensively branched stem several feet long, which may be partly underground, and is then colourless and leafless, like a **rhizome.** From it arise secondary, upright branches which divide dichotomously and may produce terminal strobili. The stem produces adventitious roots, which arise all along the underside in **acropetal** succession, that is to say, successively towards the apex of the stem. These roots branch dichotomously. The stem above the ground is densely clothed with small leaves about 4 mm. long, which are borne in regular spiral succession, and are all alike in size and shape.

The cones are borne at the apices of the upright branches, and below each cone the branch elongates into a portion sparsely covered with leaves. The cones themselves are made up of closely set, acutely pointed leaves, which are termed **sporophylls,** and in the space between each sporophyll and the axis of the cone, a single kidney-shaped sporangium is produced.

FIG. 576.—*Lycopodium clavatum.* Fertile plant bearing strobili. Half natural size.

ANATOMY OF THE STEM

The stem anatomy is complex though not so elaborate as that of the Ferns. There is no true apical cell, but there is a rounded group of initial cells. Branching is quite independent of leaf formation, the branch rudiments appearing on the dorsal side of the growing point. Branching is thus monopodial (see p. 838) and the stem is dorsiventral. In the mature stem there is a broad cortex separated from the central stele by a **pericycle** consisting of several layers of thin-walled cells (Fig. 577).

There is no endodermis present. The **cortex** has three zones. There are peripheral and central zones of thickened sclerotic cells and a middle zone in which the cells are larger and thin-walled, containing a few chloroplasts. The single stele occupies about half the area of the section. It consists of a number of irregularly shaped, parallel plates of **xylem** alternating with bands of **phloem.** The xylem is composed predominantly of scalariform tracheids, with no vessels and no parenchymatous cells. Each xylem plate is surrounded by a single layer of parenchyma, with bordered pits on the inner walls, which lies between the xylem and the phloem. The phloem consists of sieve tubes and parenchyma only. The development of both the phloem and the xylem is **centripetal,** that is, from the outside towards the interior. The protoxylem, which consists of spiral and annular tracheids of small diameter, will thus be seen at the outer edge of each xylem mass, that is to say, in the **exarch** position.

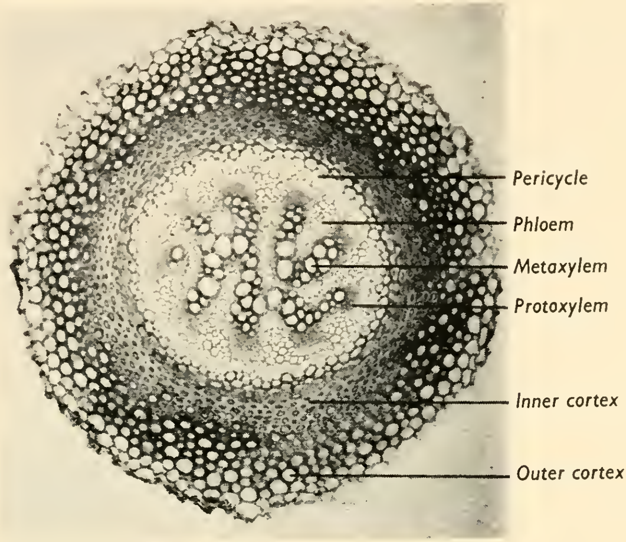

Fig. 577.—*Lycopodium clavatum.* Transverse section of the stem showing the xylem plates with external protoxylems.

Anatomy of the Leaf

The leaves are arranged in a close spiral. They are small, evergreen and lance-shaped, with a distinct point or **awn,** and tend to turn upwards from the creeping stem. In *Lycopodium complanatum* and in one or two other species the leaves are arranged in four rows, two large and two small, as in *Selaginella.* The margin may be slightly serrated and the lamina is traversed by a midrib which does not quite reach the apex. This midrib is composed of a small number of very thick-walled spiral tracheids, surrounded only at the base of the leaf by a rather irregular row of sieve tubes (Fig. 578).

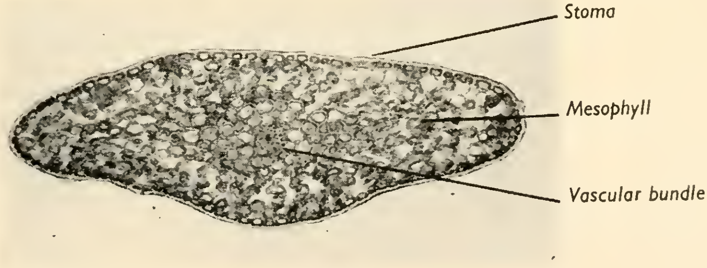

Fig. 578.—*Lycopodium clavatum.* Transverse section of the leaf.

Sclerenchyma surrounds the bundle, but no endodermis can be recognized. The leaf traces are given off from the protoxylems at the outer margins of the xylem plates in the stem and make no leaf gap in the stele as they leave it.

The lamina shows no apical growth, as do Fern leaves. The highly cuticularized epidermis contains no chlorophyll, but has stomata, usually on both sides of the leaf. The mesophyll tissue is very spongy and undifferentiated.

Anatomy of the Root

The roots of the mature plant are all adventitious and are borne ventrally on the stem, arising in acropetal succession, but without any definite spacing or relationship to other organs. They are produced **endogenously** from the pericycle and they branch dichotomously (Fig. 579). No lateral roots are formed, but root hairs arise in pairs, as the result of oblique divisions in the surface cells. There is an apical meristem and a **root cap** is developed, as in Angiosperms (see p. 794).

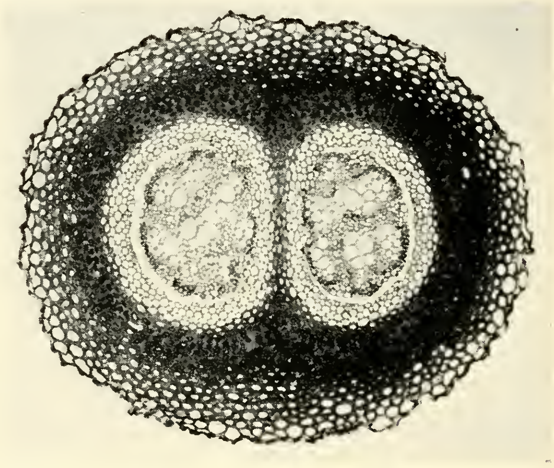

Fig. 579.—*Lycopodium clavatum.* Transverse section of an old root showing dichotomy. Note the similarity of the stelar anatomy to that of the stem.

The anatomy of the mature root differs very little from that of the stem, though the stele is smaller and simpler. There are from seven to ten protoxylems, and the corresponding metaxylem masses often unite in the centre, presenting a stellate form, with the phloems between the rays. Smaller roots may be only diarch. The close similarity of anatomical structure between the stem and the root is very interesting morphologically, as it indicates the unity of the axis in all its parts, whether leaf-bearing or not. This is clearly shown in *Lycopodium* because the leaves are too small to affect the stem anatomy to any great extent. The alteration of stem structure seen in Ferns and higher plants, where it differs markedly from that of the root, may be due to the much greater development of the leaves and leaf traces in these forms.

Development of the Strobilus

The **strobili** occupy the ends of erect branches called **podia,** which are radially symmetrical and which bear small leaves spaced at intervals from one another, contrasting sharply with the closely spiral strobilar leaves or **sporophylls,** upon which the sporangia are produced. Each podium normally bears two strobili, on axes produced by a dichotomy of the apex. The strobili are 3 to 6 cm. long, and being carried at the end of the upright podia are favourably placed for wind dispersal of the spores.

Each sporophyll bears one large **sporangium** on its upper surface, close to the base (Fig. 580). All the sporangia are alike and each contains numerous small **spores.** The sporophylls have broad bases and closely overlap, so that the sporangia are well protected. The sporophylls are adapted only to bear and protect the sporangia. They have little or no chlorophyll, though stomata are present. Each bears a dorsal outgrowth, directed downwards, which fits between the sporangia below and helps to protect them. A remarkable feature of the anatomy of the sporophyll is the presence of an area of disintegrated cells which appears to represent a parichnos like that in the leaves of *Isoetes* and *Lepidodendron.*

The sporangium arises from a transverse row of cells on the surface of the sporophyll (Fig. 581). These, by division, give rise to a **wall,** three cells thick, the innermost of which becomes the **tapetum** or nourishing layer for the spores. Centrally there is the **archesporium,** consisting of three tangential rows of twelve cells each, from which, by further divisions, arise the **spore mother cells.** These undergo meiosis and produce tetrads of monoploid **spores.** Below the archesporium the wall forms a pad of sterile tissue which grows up in the form of cellular processes among the spores and provides the basal portion of the tapetum. The bottom of the sporangium forms a short, thick stalk or **sporangiophore.**

The mature sporangium is about 2 mm. across and is kidney-shaped. It opens by a tangential slit across the top and the spores are scattered by the wind. They settle on the ground and each germinates into a **prothallus.** The spores are yellow and are beautifully reticulated on the outer surface. Each is also marked with a triradiate ridge, along which the wall opens when the spore germinates, which may, however, be delayed for several years.

Development of the Prothallus

The prothallus in *Lycopodium clavatum* differs considerably from that in the Ferns. In the first place it is a subterranean structure, solid and tuberous, which takes from six to fifteen years to mature. Like the prothallus of *Botrychium* it is colourless and saprophytic and contains a mycorrhizal Fungus (Figs. 582 and 583).

The structure of the prothallus varies greatly in the different species of *Lycopodium*. In *L. clavatum* it is a much convoluted structure 1 to 2 cm. long, with a pointed basal part. The surface is covered with an epidermis, inside which is a cortex of several layers, followed by a palisade tissue composed of a single layer of elongated cells. These outer layers contain the endophytic Fungus. This is followed by a central tissue of hexagonal cells whose function is to store up food material. All these tissues form a wedge-shaped structure which has a more or less flat top. The core of the wedge and the

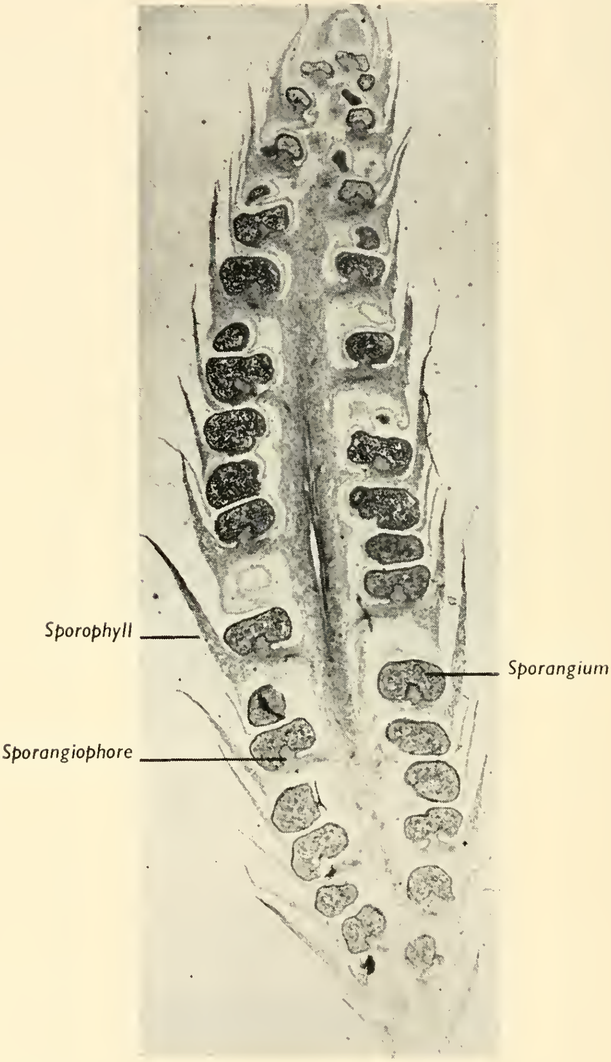

FIG. 580.—*Lycopodium clavatum*. Longitudinal section of the strobilus showing origin of the sporangia from the upper surface of the sporophylls.

irregular upper face are made up of parenchyma, which also forms a prominent rim round the top. Unicellular **rhizoids** are formed on the under surface. All the top surface is devoted to the production of the sex organs. It is called the **generative tissue,** and its cells contain no food reserves and remain for some time meristematic. The antheridia develop in the median portion and the archegonia towards the outer rim. The development is centripetal.

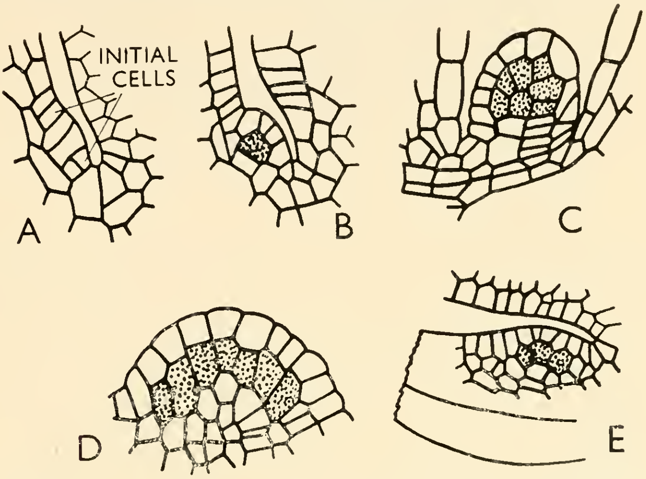

FIG. 581.—*Lycopodium.* Origin of the sporangium. A, Superficial group of initial cells. B, Archesporial mother cell. C, Development of archesporium and beginning of sporangiophore. D, Tangential section of young sporangium at slightly later stage than B, showing curved row of archesporial mother cells. E, Sporangium initial in radial section showing three rows of archesporial mother cells. A to D, *L. selago.* E, *L. clavatum.* (*After Bower.*)

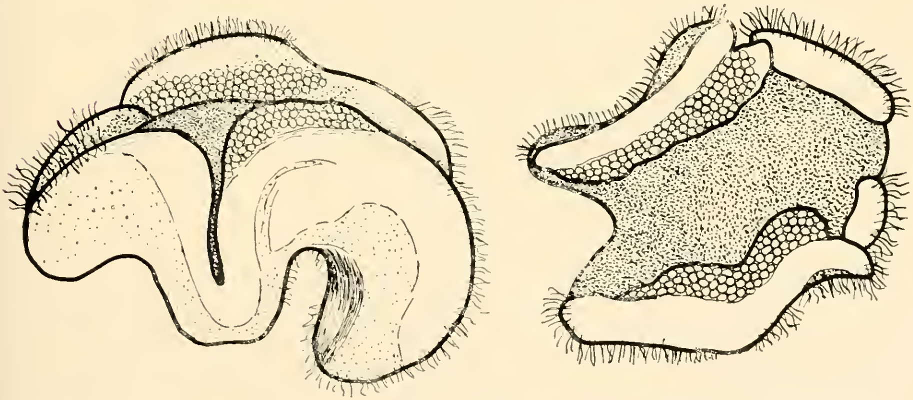

FIG. 582.—*Lycopodium clavatum.* Side and top aspects of mature prothallus showing numerous antheridia and rhizoids. (*After Lang.*)

The mode of nutrition of the prothallus is remarkable. The cells of the cortex and the palisade cells are filled with fungal hyphae, and these form what is termed a **mycorrhizal association** with the cells of the prothallus.

This association is probably symbiotic. The entry of the Fungus happens very shortly after the germination of the spore, and if it does not occur the prothallus never develops more than five cells. There is reason to suppose that the Fungus supplies the tissues with some nutrient material, but the chemistry of the relationship is unknown.

As a few species of *Lycopodium*, notably *L. cernuum*, have surface-living prothalli with chlorophyll, it seems probable that the mycorrhizal habit has originated secondarily, with loss of chlorophyll, though whether the underground growth is the cause or the effect of the change cannot be ascertained.

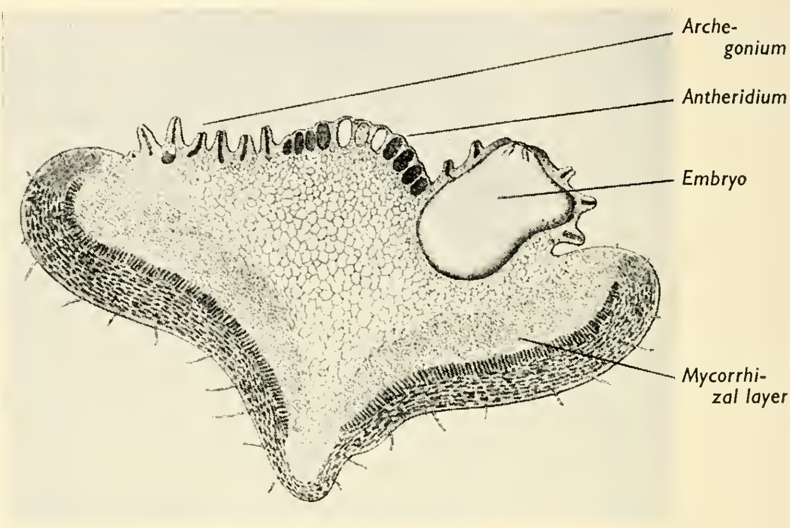

FIG. 583.—*Lycopodium clavatum.* Vertical section through the prothallus showing mycorrhizal zone and reproductive organs. (*After Bruchmann.*)

DEVELOPMENT OF THE ANTHERIDIUM

The **antheridium** arises from a superficial cell of the prothallus. This divides into an inner cell, from which the **antherozoid mother cells** are formed, and an outer cell which produces the covering layer of the antheridium. The mature antheridium consists of an oval mass of antherozoid mother cells projecting slightly from the prothallial tissue and surrounded by a wall, which is partly formed by the covering layer and partly from prothallial cells (Fig. 584).

The **antherozoids** are biflagellate and closely resemble those of the Bryophyta (Fig. 585). This is peculiar to the order Lycopodiales among Pteridophyta and suggests a closer linkage with the Mosses than with the Ferns. The character, though minute, is highly significant from the point of view of relationship, because it is not correlated with any other peculiarity of structure or function in the species.

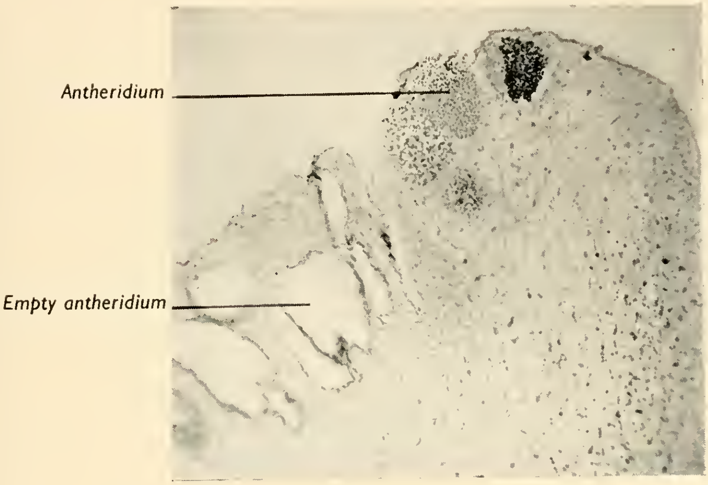

Fig. 584.—*Lycopodium clavatum.* Vertical section of prothallus showing young and old antheridia.

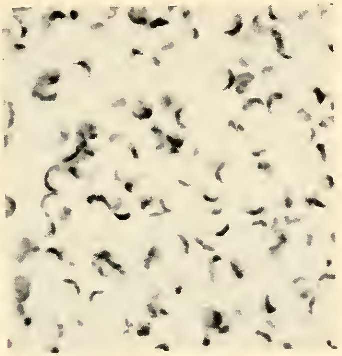

Fig. 585.—*Lycopodium clavatum.* Antherozoids from Fig. 584. Greatly enlarged.

Development of the Archegonium

The archegonia develop on the same prothallus as the antheridia, but towards the margins. Many archegonia are normally formed, but only one develops after fertilization. The **archegonium** arises from a superficial cell which divides into two. The outer cell forms the **neck,** which is here long and straight, as in the Bryophyta. The inner cell divides again, into a **primary canal cell** and a **primary ventral cell.** The former gives rise to about six **neck canal cells,** while the latter probably functions directly as an **oosphere.** The resemblance to the Bryophyta in these homosporous forms is all the more striking because in the heterosporous *Selaginella* and *Isoetes* the archegonium has undergone marked reduction in the direction of the type found in the Gymnosperms.

Development of the Embryo

The antherozoids make their way down the neck of the archegonium and one fuses with the oosphere. The resulting zygote then begins to develop, but the process is remarkably slow and the young embryo, instead of growing out towards the neck of the archegonium, pushes its way down into the prothallus in the course of development. The first division of the oosphere is transverse and separates an upper cell, the **suspensor,** which does not divide again. The lower cell divides three times, forming an **octant** or spherical group of eight cells. Two of the lower cells in this octant form the stem and two form the first leaf, expanding obliquely upwards as they develop. The four upper cells of the octant enlarge obliquely downwards to produce a tuberous mass of cells called the **foot,** which remains as an intraprothallial haustorium, deriving food from the prothallus until the embryo at length becomes independent (Fig. 586). The first root arises exogenously near the base of the first leaf, but its position is variable. Subsequent roots develop endogenously. As the stem grows it emerges from the prothallus and more leaves are formed. These first leaves have no midrib and no vascular supply. They are sometimes called **prophylls,** and it is interesting to note that in the small allied genus *Phylloglossum*, from Australia, all the leaves, even in the mature plant, are in this condition. It has therefore been called " permanently embryonic." There is no mycorrhizal Fungus in the cells of the embryo. The primary stem lasts only for a short time and is then replaced by an adventitious outgrowth from its base which becomes the horizontal stem of the mature plant.

Eventually the prothallus decays and the young embryo develops more roots and becomes entirely self-supporting. Its first vascular system is a solid protostele, and the mature stelar arrangement is developed by a process of furrowing, the phloem entering more and more deeply into the central xylem mass and dividing it into separate plates. The whole process of the embryological development is extraordinarily slow, and several years may elapse before the young sporophyte reaches the surface of the soil.

Alternation of Generations

It will be seen that the life history of *Lycopodium* does not differ in any essential way from that of the Ferns. Only in the relative importance of the gametophyte, which has become modified in response to an underground life do we see any marked difference. There is the same development of the sporophyte as an independent structure, deriving its food during its young stage from the prothallus and ultimately becoming self-supporting. The development of the sex organs and the method of fertilization are not only similar to those processes in the Ferns, but also show some relationship with those in the Bryophyta, so that we see how, in spite of superficial differences, we can compare the gametophytes of the two groups, and we realize that it is correct to regard the prothallus of the Pteridophyta as homologous with the gametophyte of the Moss or Liverwort.

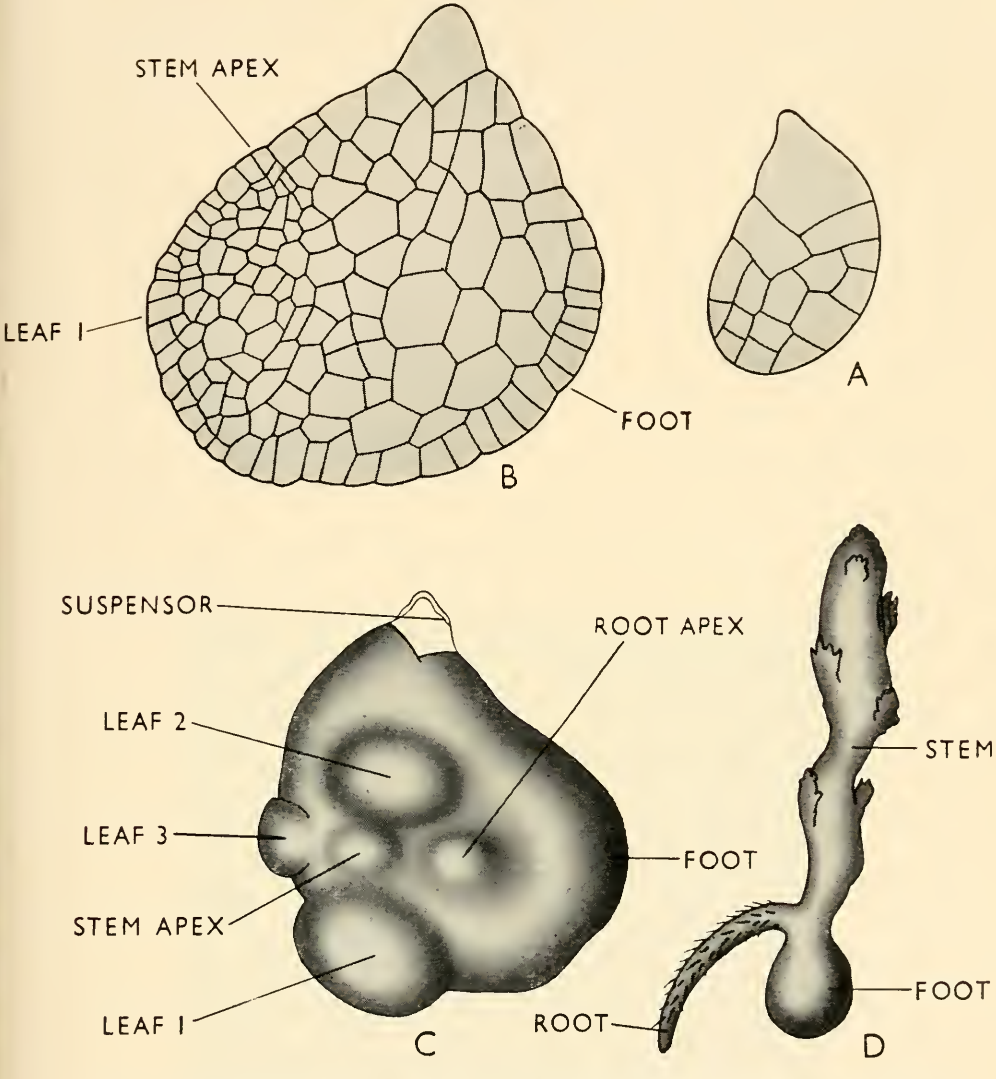

Fig. 586.—*Lycopodium annotinum.* A and B, Young embryo. C, Embryo from above, showing origin of leaves and primary root arising from the stem apex. D, Young plant with foot and stem with reduced leaves. (*After Bruchmann.*)

The life history of *Lycopodium clavatum* may be illustrated graphically by the diagram overleaf (Fig. 587).

Selaginella kraussiana.

This species of *Selaginella* is not a native of this country, but occurs commonly in South Africa and the Azores. It is, however, cultivated very frequently in greenhouses, where it reproduces itself very readily, and it is naturalized in one or two places in Britain (Fig. 588).

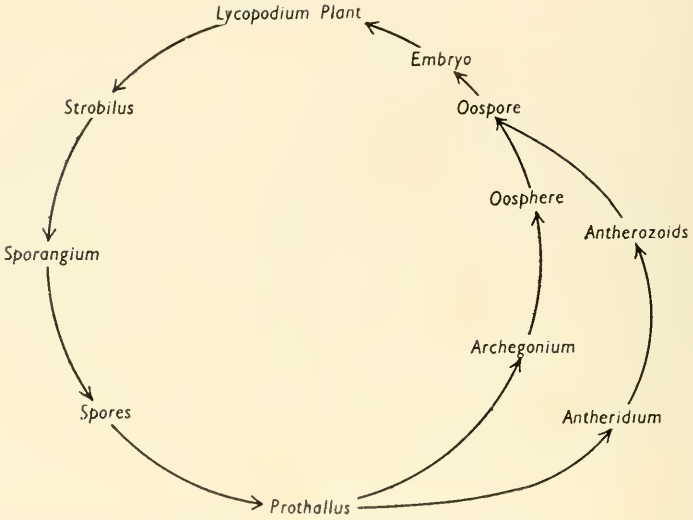

FIG. 587.—Life-cycle of *Lycopodium clavatum.*

FIG. 588.—*Selaginella kraussiana* showing prostrate habit and rhizophores bearing roots. Half natural size.

The stem is trailing, up to 30 cm. long and richly branched. Young branches develop so quickly that they seem at first to be equal to the main axis, thus giving an appearance of perfect dichotomy, which, however, is not the case. The main apex has two, four-sided, apical cells, but the side branches have only one, which is three-sided, and is formed from a segment of one of the main apicals. They are thus truly lateral and the branching is monopodial. The side shoots also branch freely in the same way, the young branches all lying in the same plane and forming a flat, pinnate frond.

Older branches turn up vertically. The stem is clothed with leaves which are arranged in four rows, the leaves being in pairs, each pair consisting of a large and a small leaf. Those springing from the lower surface are considerably larger than those originating from the upper surface. In this way all the leaves are exposed equally to the light, and the lower leaves are not overshadowed by the upper ones. At the base of each young leaf is a small membranous outgrowth called the **ligule** which soon withers away. This structure is characteristic of this family of the Lycopodiales. As it is also present in some of the fossil tree-like forms, it is considered as good evidence of the close relationship between these fossil trees and the small present-day species of the genus *Selaginella*, and it is concluded that during the Carboniferous period the group was of far greater importance than it is at the present time.

Arising at the base of each branch is a root-like organ, which is called a **rhizophore.** This structure resembles a root in being leafless, but it differs in not possessing a root cap. In *S. kraussiana* it only reaches a length of a few millimetres when it loses its apical growth and produces two equal roots, which arise endogenously from cortical cells, thus simulating dichotomy. If the rhizophore subsequently elongates, as it may in damp air, its growth is intercalary. The roots produced grow downwards and on entering the soil again branch and develop root hairs. The leafy stem itself bears no roots. In epiphytic species of *Selaginella*, which may reach a length of many feet, climbing among branches, the rhizophores are very important in carrying the root system into deep crevices where moisture is held.

From the stem certain vertical branches grow up which differ in structure from the ordinary stem, since on them are borne the reproductive organs. As in *Lycopodium* these organs are called **strobili** and their leaves **sporophylls.** The sporophylls, like the vegetative leaves, are borne in opposite pairs, but all are the same size. In *Selaginella*, the sporophyll bears a single **sporangium** in the axil between the leaf and the stem. These sporangia are of two kinds, **megasporangia** and **microsporangia.** The former encloses a small number, generally four, of large **megaspores,** while the latter bear a large number of small **microspores.** *Selaginella* is therefore an example of an **heterosporous** plant. In most species both types of sporangia are produced on the same strobilus. In *Selaginella kraussiana* the microsporangia are usually produced in the axils of the upper sporophylls while the megasporangia are developed in the axils of the lower sporophylls.

Anatomy of the Stem

In section the stem is dorsiventral, flattened above and rounded below, with two lateral grooves (Fig. 589). There may be one or several **steles** in the stem, according to the species, and in *Selaginella kraussiana* there are two steles, each of which has one or sometimes two protoxylem groups at the ends of the oval mass of **xylem,** which is therefore **exarch.** There is a certain amount of parenchyma between xylem and phloem. The **phloem** forms a ring round the xylem. It is similar in structure to that of the Ferns and contains a small amount of phloem parenchyma. Surrounding the phloem is the single-layered **pericycle.** The xylem elements are all tracheids in the present species, but in *S. rupicola* and one or two other species true vessels are formed.

The stele is separated from the cortex by a well-marked annular space, like that around the spore layer in a Moss capsule. As in the latter case the space is bridged by a number of **trabeculae,** which are at first unicellular, but later become divided into slender rows of cells by which the steles are supported. They are generally regarded as the **endodermis,** and they may show a cutinized belt around the first cell in the early stage. The **cortex** is composed of thin-walled parenchyma cells without air spaces. The cells contain chloroplasts united in chains and obviously derived from a single original plastid, of which a rudiment occurs in the meristem cells. On the outside is the **epidermis,** which consists of elongated, pointed cells, without stomata. The steles run parallel to each other, but they unite below each branch and separate again above it (Fig. 590). The space between them has been interpreted as a branch gap, corresponding to the leaf gaps in the Ferns. The leaf traces in *Selaginella* make no gaps in the stele.

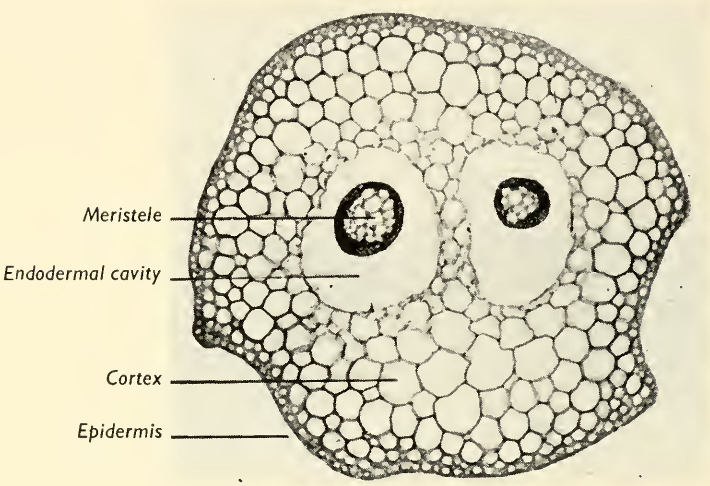

FIG. 589.—*Selaginella kraussiana.* Transverse section of the stem showing two steles surrounded by endodermal cavities. Trabeculae are not shown in this section.

ANATOMY OF THE LEAF

The leaf is entire, small and simple in structure. Stomata are confined to the lower surface. The epidermal cells and the assimilatory cells of the mesophyll have each only a single, very large chloroplast, sometimes more or less divided into two, recalling the condition in *Anthoceros.* The mesophyll is not differentiated into palisade and spongy tissue, but is very open and lacunar throughout. A single leaf trace passes into the leaf from the stem and forms an unbranched midrib. It is concentric in structure, composed of a central strand of xylem surrounded by phloem and an endodermis. The leaf traces originate, as in *Lycopodium*, from the protoxylem group.

ANATOMY OF THE RHIZOPHORE

Each rhizophore originates from the *upper* surface of the stem, at the point where a branch is attached. It grows downwards for a short time by means of an apical cell, but very soon this is lost and two root apices are differentiated from sub-epidermal cells (Fig. 591). These roots do not at first develop, but the rhizophore continues to elongate by intercalary growth until the soil is reached, when the roots emerge and produce root hairs. Subsequent root branching is monopodial, but, as in the stem, looks dichotomous. The lateral rootlets also originate from sub-epidermal cells of the main roots. They are not therefore truly endogenous, as are nearly all other roots.

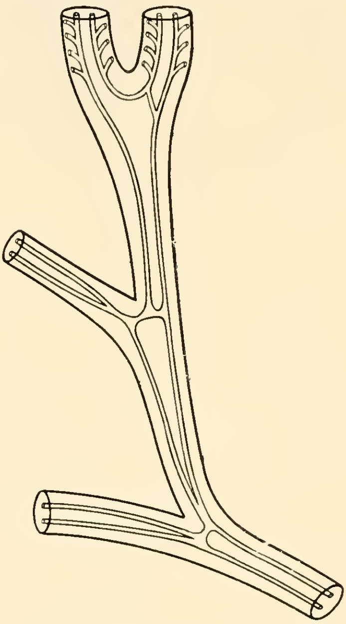

FIG. 590.—*Selaginella kraussiana.* Transparent view of the stem showing bifurcation of the stele at the branch nodes. Leaf traces only shown at the top of the figure. (*After Harvey Gibson.*)

The vascular structures of both rhizophore and root are similar (Fig. 592). There is a single concentric stele, with one protoxylem, which is central in the rhizophore and at one side in the root. The root also has a good endodermis, while that of the rhizophore is vague. The phloem surrounds the xylem strand, but in the root there are no sieve tubes opposite the protoxylem.

THE SPORANGIA

The sporangia arise from a group of cells on the surface of the axis, close to the base of each sporophyll.* The sporophylls closely resemble the vegetative leaves in structure, and each has on its upper surface a **ligule,** in the form of a small scale which develops from an epidermal cell close to the abaxial side of the sporangium. It has a distinct foot or **glossopodium,** which remains embedded in the tissue of the sporophyll. The ligule matures before the sporangium and withers when the latter is ripe. Its cells are

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* We have retained the term sporophyll, as applied to the strobilar leaves of *Selaginella,* in deference to general usage. The sporangia are not, however, borne on the leaves but on the axis, a condition described as **stachyosporous,** in distinction from the condition in, *e.g., Lycopodium,* which is truly **phyllosporous.**

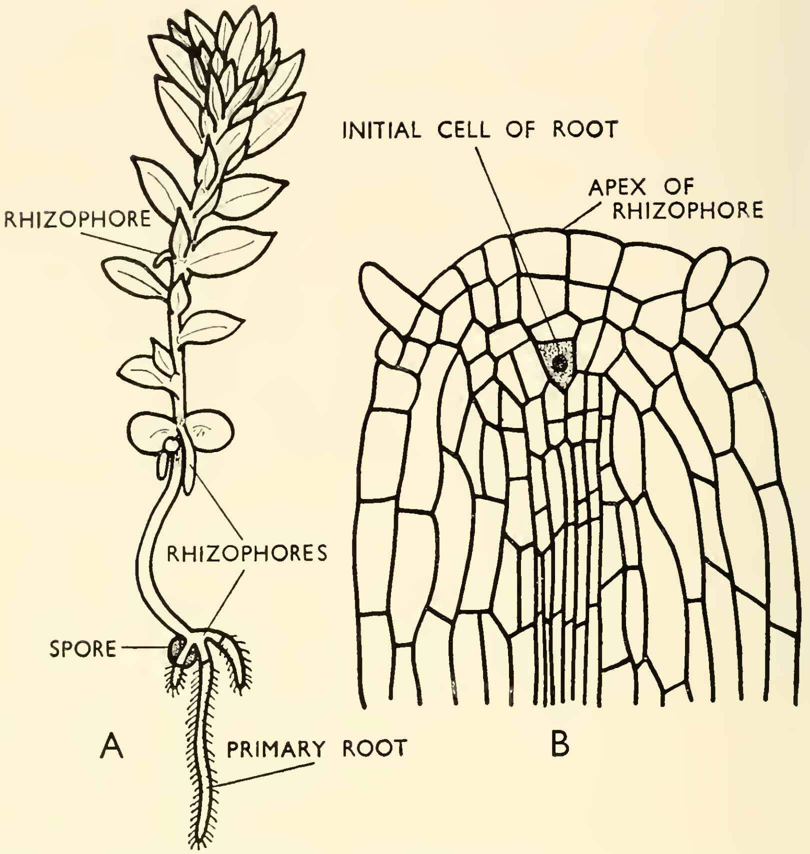

FIG. 591.—*Selaginella martensii.* A, Young sporeling showing primary root and origin of rhizophores. The small dorsal leaves are clearly shown. B, Longitudinal section of apex of rhizophore showing endogenous origin of root initial. (*After Goebel.*)

mucilaginous and probably secrete water which keeps the young sporangium moist (Fig. 593).

The early development of both kinds of sporangia is identical and closely follows that in *Lycopodium*, up to the mother-cell stage. The wall is only two cells thick but there is in addition a lining of a single layer of nutritive cells forming the **tapetum.** The colour of the spores shows through the translucent wall, the microsporangia being whitish-green and the megasporangia orange.

In the microsporangia some of the mother cells abort, but a large number develop and form tetrads of **microspores,** which are tetrahedral in shape, cutinized, ornamented with papillae and furnished with a triradiate ridge marking the line at which the spore eventually opens, or dehisces. In the megasporangia all the mother cells abort except one. This produces four **megaspores** which are nourished by the degenerating cells and the tapetal fluid, and grow to such a size that they distend the sporangial wall and even displace the sporophyll. The megaspores are similar in shape to the microspores but about twenty times as large, being easily visible to the eye. They have a very thick, cutinized wall, which is rough and warty on the outside, and they also have a very marked triradiate ridge which is prolonged into a beak, at which point dehiscence of the spore later occurs. The mature megaspores are so arranged in the megasporangium that these beaks converge together in the centre of the sporangium. In both cases meiosis occurs during the formation of the spores.

When the sporangia are ripe they dehisce by a tangential slit across the top and the two halves gape apart. The slit does not go down to the base and the contraction of the unsplit basal portion, as it dries, forces the spores out with some violence, so that they fall a few centimetres away from the parent plant. This action is much more powerful in the megasporangia, where the contraction is increased by the presence of a band of thin cells which acts as a hinge between the two contracting sides of the sporangium. This dispersal mechanism may serve to bring spores from different plants into proximity and so promote cross-fertilization.

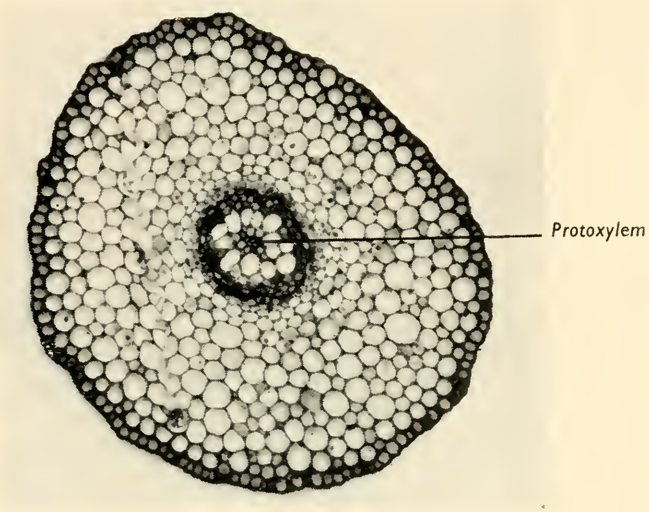

FIG. 592.—*Selaginella kraussiana.* Transverse section of the rhizophore showing the simple concentric stele with internal protoxylem.

The great difference in spore size is correlated with a differentiation in sex. The microspores produce only male prothalli, with antherozoids. The megaspores are purely female, and their large size allows for the storage of food material, in reserve for the nourishment of the young embryo. *Selaginella* thus marks a very important stage in the evolution of sex in plants and provides an example, among living Cryptogams, of an approach towards the seed habit of the higher plants. *Selaginella* itself is not genetically related to the seed plants, but their true ancestors in Palaeozoic times must have passed through an early stage to which *Selaginella* yields the clue. In fact the plant provides us with a link between the two great groups, Cryptogams and Phanerogams, which helps us to understand how they are related.

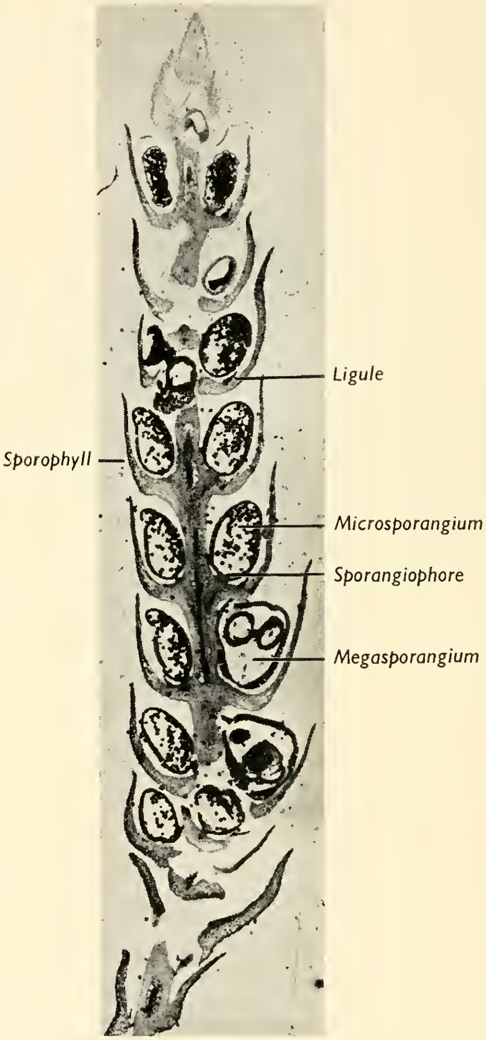

Fig. 593.—*Selaginella kraussiana.* Longitudinal section of the strobilus showing the arrangement of the megasporangia and microsporangia.

The Male Gametophyte

In *Lycopodium* the prothallus is reduced to a saprophytic underground structure, but in *Selaginella* the reduction of the gametophyte generation has gone further, as the prothalli do not even emerge from the spores. Both prothalli are consequently minute, though the female is less reduced than the male.

The contents of the microspore divide into two cells of very unequal size. This is accomplished before the spores are shed. The smaller cell is called the **prothallial cell** and takes no further part in development (Fig. 594). It appears to be all that represents the vegetative part of the prothallus.

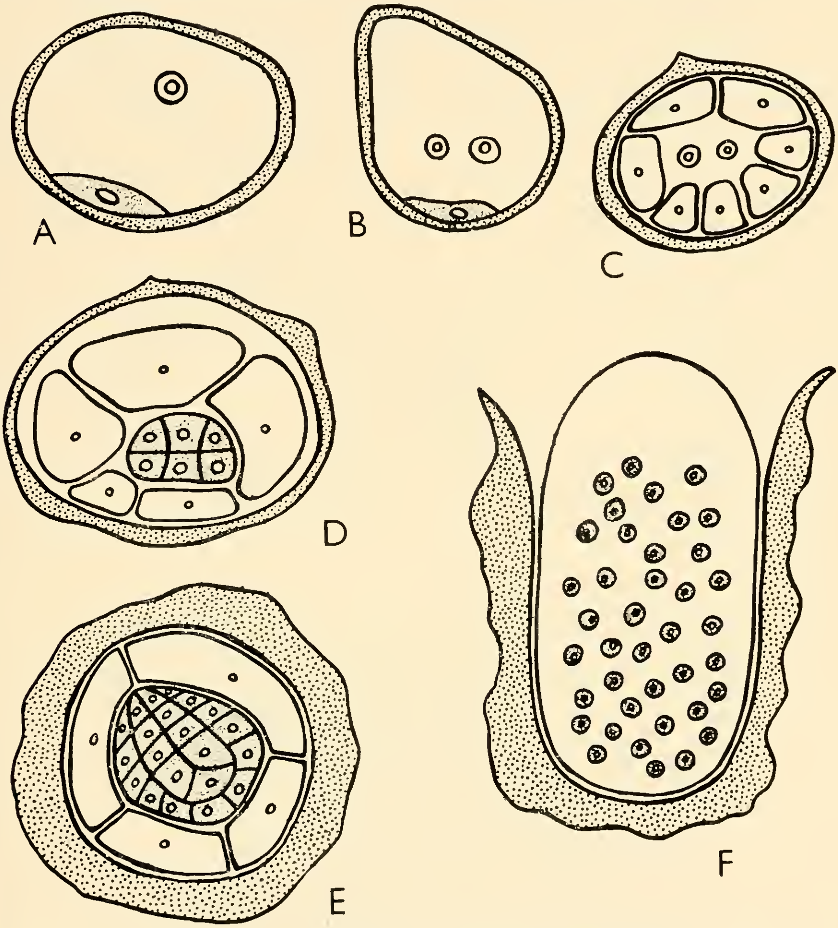

FIG. 594.—*Selaginella apoda.* Development of the male gametophyte. A, Section of the microspore showing division of contents to form lenticular prothallial cell, the remainder constituting the antheridial cell. B, First division of the nucleus of the antheridial cell. C, Differentiation of the antheridial wall cells. D and E, Differentiation of the antherozoid mother cells. F, Dehiscence of the microspore to release the antherozoids. All cell walls have disappeared. (*After Lyon.*)

The larger cell, which is called the **antheridial cell,** continues to divide until a group of twelve cells is formed. Of these, eight form a wall enclosing a group of four central cells. Whilst these changes have been going on within the spore, its outer wall bursts at the triradiate ridge, so that the outer end of the developing tissue is only covered by a thin cellulose wall. The central cells now undergo a number of divisions, forming a mass of 128 tiny cells lying freely in a space formed by the breakdown of the outer cells. This structure we regard as an antheridium, the eight outer cells forming its wall, and the central cells representing the **antherozoid mother cells,** from each of which at maturity an **antherozoid** develops. The antherozoid is an

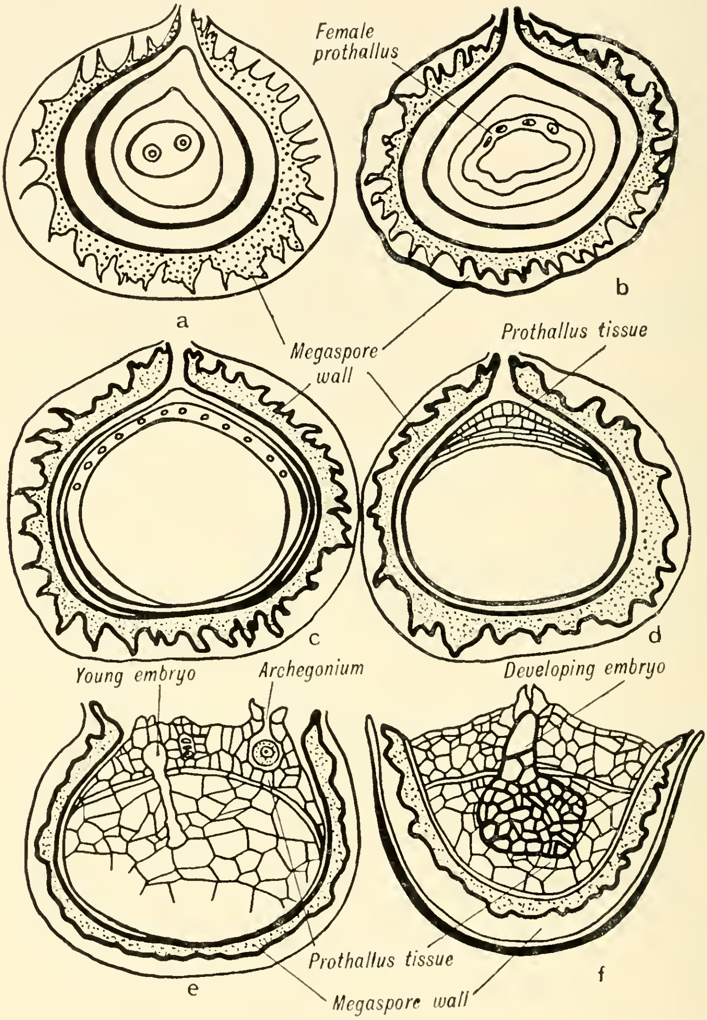

Fig. 595.—*Selaginella kraussiana.* Development of the female gametophyte. A and B, Early stages showing contracted protoplast and exospore and mesospore separated by a space containing a gelatinous membrane. C, Protoplast expanded forming a hollow sphere in the megaspore. Nuclei arranged apically and increasing in number. D, Protoplast beginning to thicken to fill the central space and dividing apically into female gametophyte cells. E, Mature gametophyte bounded below by the diaphragm, the remainder of protoplast dividing into cells. F, Embryo with suspensor, developing in nutritive tissue below the diaphragm.

elongated body, at one end of which two long flagella are produced. The antherozoids escape by the bursting of the thin cell wall at the upper end of the microspore and swim away in the film of water which normally covers the damp soil in which these plants live. The development of the male prothallus often begins before the spores are shed and is completed on the ground.

THE FEMALE GAMETOPHYTE

Meanwhile the megaspores have also germinated. In fact their development also has already begun before the megaspores have been shed from the megasporangium.

At an early stage of development the protoplast contracts to a small sac and the wall rapidly expands, so that a wide space separates them. At the same time the spore wall separates into two thick layers, the **exospore** and the **mesospore,** separated by a space containing a gelatinous membrane. At this stage there is only one monoploid nucleus, but this soon begins to divide repeatedly until a large number of nuclei are distributed round the protoplasmic layer. The protoplast now rapidly increases both in size and thickness, pressing the two spore coats into contact once more and gradually filling up all the central vacuole with cytoplasm.

At the apex of the spore, that is towards the centre of the tri-radiate ridge, delicate walls begin to appear in the cytoplasm, dividing it into cells, which form a lens-shaped layer, three cells thick in the middle but only one cell thick at the sides. This is the **female prothallus** (Fig. 595). Below

FIG. 596.—*Selaginella sp.* Vertical section of a megaspore containing developed female prothallus.

the prothallus some rather vague walls extend downwards into the rest of the protoplasm, but without dividing it completely into closed cells. The bottom of the prothallus itself becomes thickened, and it is thus clearly separated from the material below. The thickened layer is called the **diaphragm** (Fig. 596).

Certain cells now begin to enlarge to form archegonia, and at this stage the spore opens along the ridge, exposing the prothallus. Three little protrusions are formed on its surface, which develop rhizoids (Fig. 597), but they are purely vestigial, as the prothallus is never independent. Numerous **archegonia** are formed. They are of a simple type, the initial cell dividing only into two, not three as in *Lycopodium*. The upper cell forms a short **neck,** two cells high, and the lower cell divides into the **oosphere,** the **ventral canal cell** and a single **neck-canal cell** which penetrates into the neck.

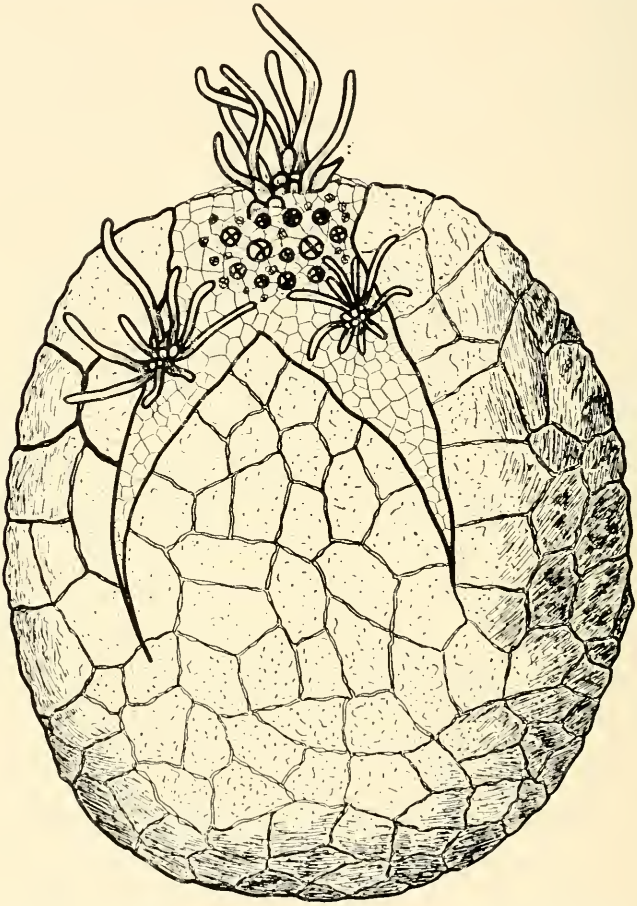

FIG. 597.—*Selaginella kraussiana*. Dehiscent megaspore showing exposed prothallial tissue with rhizoids and scattered archegonia.

Fertilization is effected by the passage of the antherozoids down the neck of the archegonium, and the fusion of one male nucleus with that of the oosphere. Prior to this the neck canal cells and the ventral canal cell have disorganized.

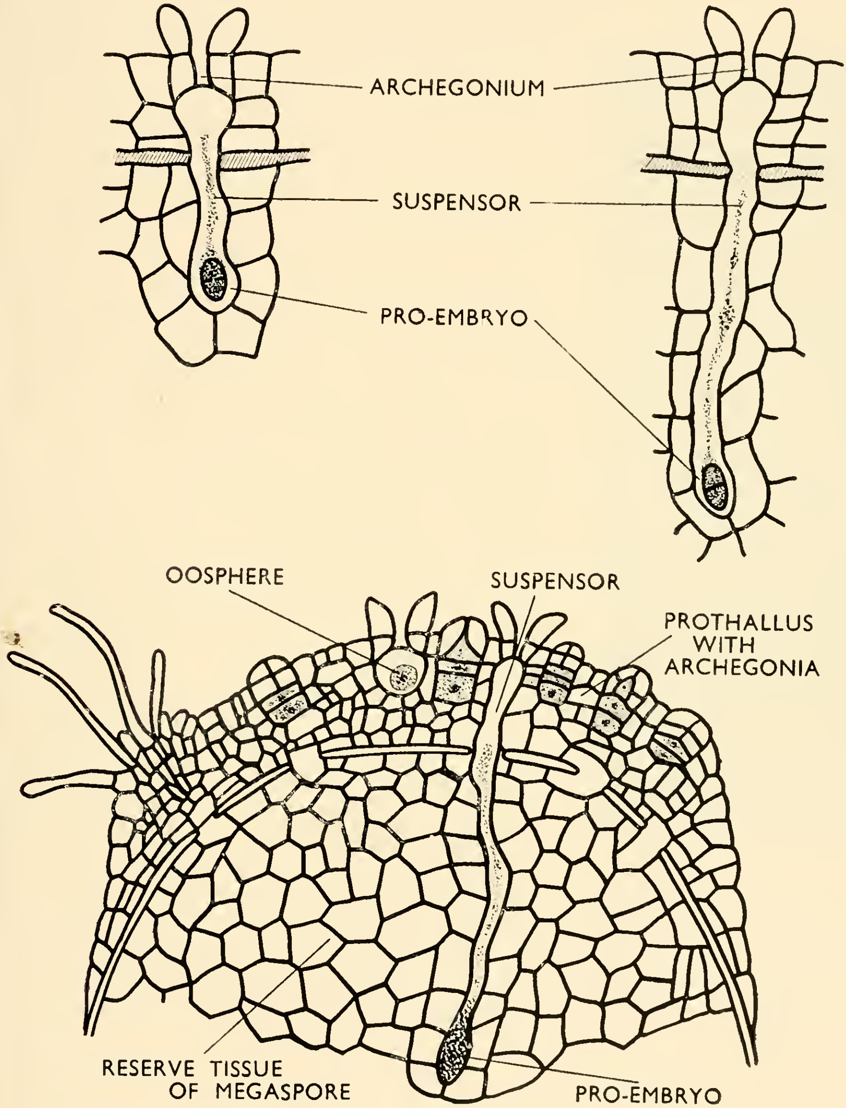

Fig. 598.—*Selaginella kraussiana* showing development of the embryo from the fertilized oosphere, penetrating into the reserve tissue. (*After Bruchmann.*)

Development of the Embryo

After fertilization the oosphere becomes surrounded by a wall and may then be regarded as an **oospore.** The oospore divides into two cells by a transverse wall. The upper cell, which lies nearest to the neck of the archegonium, forms the **suspensor** ; the lower cell alone forms the **embryo.** The suspensor cell elongates remarkably, penetrating the diaphragm and carrying the embryo down into the lower part of the spore (Fig. 598). As the embryo develops, the division of the remainder of the spore-protoplasm into cells is completed, in a way which clearly recalls the formation of endosperm in the Angiosperms.

At a slightly later stage we can recognize the following structures in the embryo. At the lower end, opposite the suspensor, lies the stem apex, marked by a wedge-shaped cell, enclosed on either side by the first two leaves or **cotyledons.** On one side a little further back is a large swollen mass of tissue, the **foot,** which is the chief organ of food absorption, whilst a little later the **radicle** becomes differentiated between the foot and the suspensor. The development of the foot pushes the stem apex to one side so that the axis of the embryo is horizontal with reference to the suspensor. In this position it develops until both ends of the axis have grown beyond the limits of the prothallus, when the root turns down and the shoot upwards. The embryo remains for some time attached to the megaspore, drawing nourishment from it. It looks very like an Angiospermic seedling attached to a seed (Fig. 599).

The two cotyledons are rather larger than the subsequent leaves. The stem below them grows until it may be a couple of centimetres long. It is called the **hypocotyl.** Above the cotyledons the young stem may grow for a short distance unbranched, but it usually divides immediately into two by the division of the apical cell. This is the only true dichotomy in its life history and it is marked by the transformation of the apical cell from a wedge shape into the four-sided cell characteristic of the mature stem.

FIG. 599.—*Selaginella kraussiana.* Young sporeling showing megaspore from which arises a young shoot showing the first dichotomy and three rhizophores, the longest of which has produced two roots.

ALTERNATION OF GENERATIONS

The most interesting point of difference between *Selaginella* and the types we have so far considered lies in the presence of two types of spores and the two distinct forms of prothalli which develop in them. The life-cycle, therefore, is more complex than in our previous example and may be represented by the following scheme (Fig. 600) :—

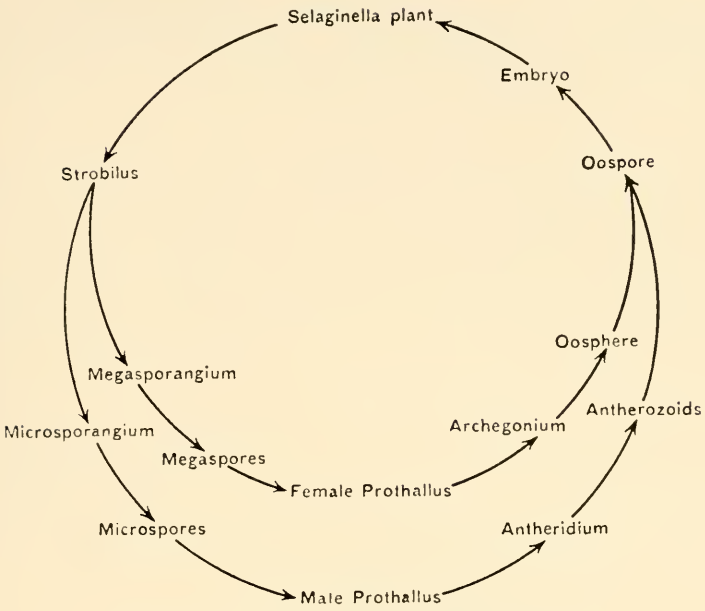

FIG. 600.—Life-cycle of *Selaginella kraussiana*.

It will be seen, however, that there is still the same alternation of generations between a sporophyte and a gametophyte, although the gametophyte is entirely dependent upon the sporophyte for its food. A great reduction in the size of the gametophyte has also occurred, especially in the male, which is represented by a single prothallial cell and a single antheridium. Since the only function of the male prothallus is to supply a number of motile antherozoids this reduction is understandable, moreover, since the only important part of the antherozoid is its nucleus and its life is very short, there is no necessity for the accumulation of a large amount of food reserve. In the female gametophyte, however, the provision of a good reserve is necessary for the nourishment of the embryo which will be supplied from it. The female prothallus is therefore associated with a considerable amount of nutriment stored in the protoplasm of the large megaspore. Its peculiar development and its lack of chlorophyll remove it a long way from the independent prothallus of *Dryopteris*. At the same time, since the structure of the archegonium is similar to that in Fern types we must regard the two structures as homologous.

The heterosporous condition illustrated by *Selaginella* constitutes one of the most important phases in the evolution of plants, and as we pass further up the evolutionary series we shall find that there is a further reduction in the number of the megaspores until only one megaspore is formed in each megasporangium. This has occurred even in some species of *Selaginella*, such as *S. apoda*, which has advanced almost to the rank of a Seed Plant, as the megaspore is retained in the sporangium and is fertilized and develops its embryo while still attached to the sporophyte. In *Selaginella*, therefore, we find for the first time that complete dependence of the gametophyte on the sporophyte which marks the Flowering Plants.

Isoetales

This is a **monotypic** order, that is, it contains only one genus, *Isoetes*, the characters of which are therefore those of the order as a whole. As in some other related orders, we can trace the ancestry of this plant back to Palaeozoic times, and insignificant as it appears to-day, it is probably the direct descendent of the tall, columnar tree, *Sigillaria*, of the Carboniferous Period.

Isoetes lacustris (Quillwort)

Isoetes is a genus of small aquatic or occasionally terrestrial plants, with about sixty species distributed principally in the Northern Hemisphere. Our type species is not uncommon in mountain lakes in this country, especially in very soft and pure waters (Fig. 601). The stem is a blackish **corm** about the size of a small Hazel nut, bearing a crop of thin, adventitious roots below

Fig. 601.—*Isoetes lacustris* showing habit of growth. Half natural size.

and a tuft of long, quill-like leaves of pale green above. Each leaf bears a **ligule,** and most of the leaves have a **sporangium** at the base. The sporangia are **heterosporous.** In the above points it is clearly related to *Selaginella*, though there is no formation of special sporangial strobili, as in the latter genus. As there is no branching and almost all the leaves are sporophylls, the whole plant may be regarded as forming a single strobilus. The antherozoids are multiciliate, and this character shows a relationship to the Ferns, so that the systematic position of the group is somewhat obscure and isolated.

If we examine a plant towards the end of the year and remove the leaves, starting from the outside, we find, in succession, firstly, sporophylls with **megasporangia,** then sporophylls with **microsporangia** and, lastly, vegetative leaves, not yet fully developed, but otherwise exactly like the sporophylls.

The sporophylls are shed in winter and the plant begins the year with only the immature vegetative leaves. Megasporophylls and microsporophylls are developed in succession during the summer and, while the old leaves drop off, the new vegetative leaves for next season develop nearest the apex. Fertile sporophylls are not formed until the plant is four years old.

Anatomy of the Stem

The stem is usually less than 2 cm. high but is proportionally somewhat broader. Stripped of its appendages it is seen to consist of two, or rarely three, broad lobes, with a wide groove between them on each side of the stem. The two grooves meet below to form a cleft across the base. Seen from above the outline is thus markedly flattened, the diameter being roughly twice as great in the line of the lobes as it is across the grooves. The growing point is sunk in an apical depression due to the expansion of the lobar tissues.

The leaf rudiments arise alternately on opposite sides of the apex, although this simple arrangement is somewhat obscured by the very broad sheathing bases of the older leaves. Some twisting also occurs later, nevertheless the **distichous** or two-ranked order can be detected even among the mature leaves.

A transverse section of the stem shows a central protostele of peculiar structure (Fig. 602). The centre is occupied by a mixed tissue of short, reticulate tracheids and thin-walled parenchyma, which apparently represents the xylem. Around this is a layer of **prismatic cells,** which have none of the histological characters of phloem, but as this layer is continuous with the phloem of the leaf traces it probably represents that tissue in the stem. A thin cambium lies outside this layer, as it does in some Monocotyledons, and it forms secondary tissues on both sides. Inwards it produces a small number of additional prismatic cells, arranged in rings, which are probably annual. Mingled with these, however, are imperfectly formed tracheids, so that this tissue is unlike anything called phloem elsewhere. On the outside is formed an extensive zone of parenchyma, or **secondary cortex** (Fig. 603), which is formed anew every year and pushes outwards the dying remains of the zone formed the previous year, which then rots off. The cortical cells are used for storage and are filled with starch grains.

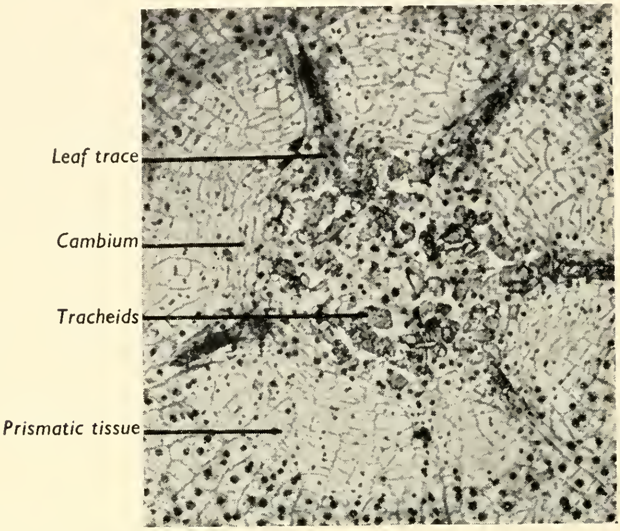

FIG. 602.—*Isoetes lacustris.* Transverse section of stem showing the structure of the stele.

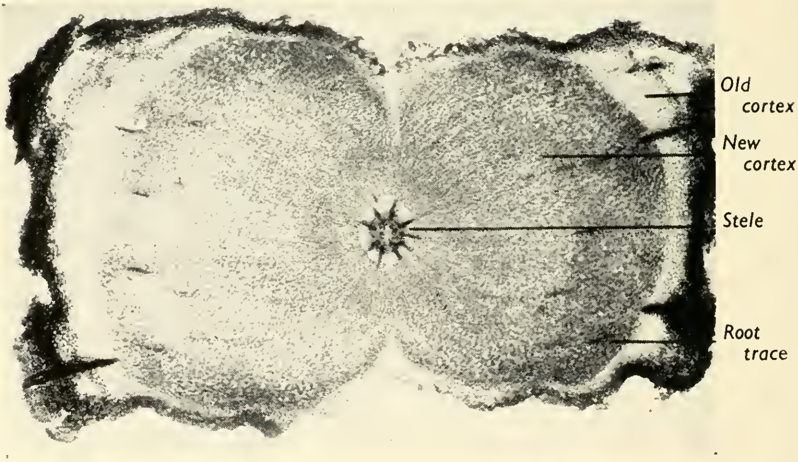

FIG. 603.—*Isoetes lacustris.* Transverse section of the entire stem showing the two-lobed structure and the replacement of old cortex by new cortex.

From the upper part of the stele arise the leaf traces, one to each leaf, which curve upwards and outwards through the secondary cortex (Fig. 604).

The stem apex though sunken between the stem lobes, is itself flat and shows no definite apical cell.* It rarely branches, but when this does occur it is as a dichotomy, in the plane of the stem grooves, and scarcely amounts to more than the formation of two short stumps.

If a longitudinal section of the stem is cut in the median plane of the stem lobes the vascular stele appears cigar-shaped, tapering above and below. It is doubtful whether any portion of it exists which is entirely distinct from the leaf traces, that is to say, is truly cauline, as in the Ferns, and indeed the whole stem structure in *Isoetes* seems subordinated to the relatively large leaves.

If, however, a longitudinal section is cut at right angles to the last, *i.e.*, in the plane of the stem grooves, the lower end of the stele is seen to expand on both sides into two remarkable, upwardly curved horns, forming a structure with an outline like that of a gardener's edging tool (Figs. 605 and 606). It is from the two flat sides of this curved portion that the roots arise. They are endogenous and are produced in definite parallel rows, in acropetal succession throughout the year.

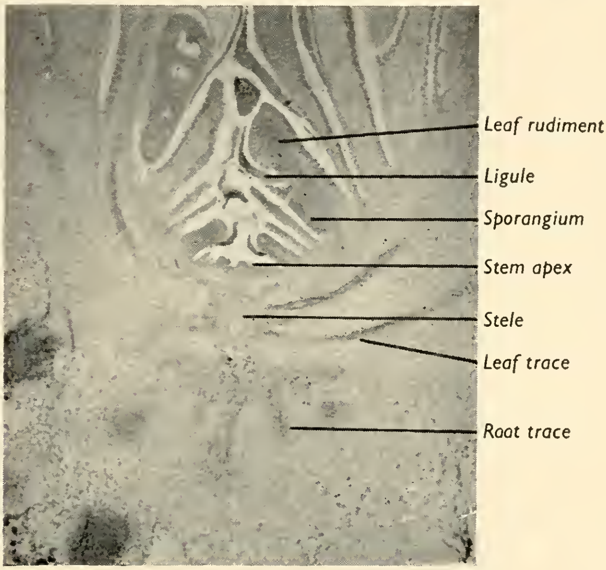

FIG. 604.—*Isoetes lacustris.* Longitudinal section through the stem apex showing leaf rudiments with prominent ligules and the compressed stele giving off leaf and root traces.

The actual cleft at the base of the stem shelters a linear meristem, which helps to build up the stem lobes and grows very slowly downwards. It is sunk in the tissues, being covered in by the fusion of the lobar parenchyma on each side. We have here a rare example of what has been called a **caudex descendens.** It has been compared to a rhizophore, probably correctly,

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* In an allied, terrestrial species, *I. hystrix*, there is probably a pair of four-sided apical cells, as in *Lycopodium.*

though it is not a branch as in *Selaginella*, but is the lower end of the main stem, taking the place of the short-lived primary root of the embryo plant.

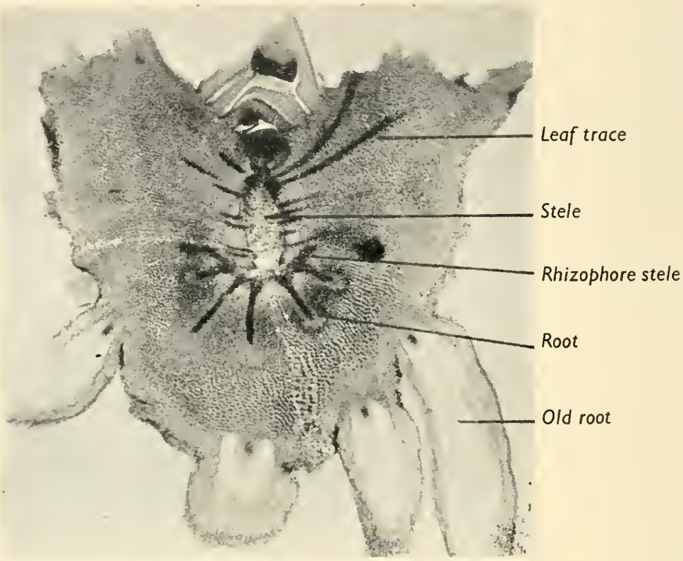

FIG. 605.—*Isoetes lacustris*. Longitudinal section of the entire stem in the plane of the grooves showing the curved rhizophore stele giving off root traces.

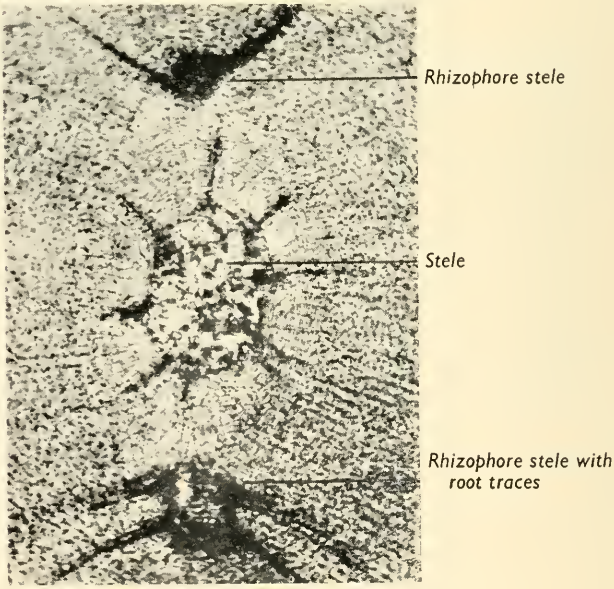

FIG. 606.—*Isoetes lacustris*. Transverse section through the lower part of the stem showing the ends of the curved rhizophore stele on each side of the main stele.

ANATOMY OF THE ROOT

The roots, like the leaves, last only for one year. Each successive row formed is pushed gradually down the sides of the cleft and out over the lower surface of a stem lobe, as the activity of the stelar cambium builds up an increasing width of secondary cortex. The first roots of the season are therefore those which lie outmost on the stem lobes, with successively younger rows inwards. In the next year a new succession of roots is begun and the old ones are discarded along with the moribund tissues of the old stem lobes.

It is specially noteworthy that *Isoetes* is the only living Vascular Cryptogam which has a permanently organised root system. In all other types, except perhaps in some species of *Selaginella*, the roots are adventitious and irregularly produced at various points. No special root-producing region exists, as in the present case.

The branching of the roots is by a true dichotomy which establishes a relationship with *Lycopodium* and the fossil Lepidodendraceae.

The root anatomy is very simple and singular among living plants, but it is highly suggestive of the affinities of *Isoetes* with the fossil Lycopods.

The chief feature is a very large central cavity surrounded by a cortex, and containing one monarch stele, of xylem surrounded by phloem, which is attached to the wall of the central cavity at one side (Fig. 607).

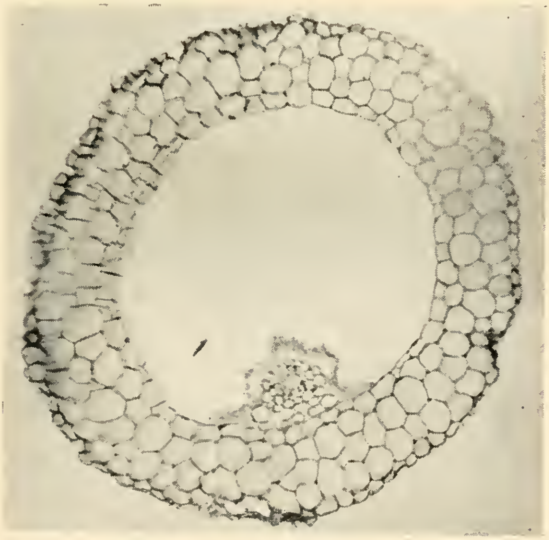

FIG. 607.—*Isoetes lacustris*. Transverse section of root showing cortex with large central cavity, at one side of which the small stele is attached.

This is almost exactly like the roots of the Lepidodendraceae, known under the name of *Stigmaria* (Fig. 608), which are so abundant in the Coal Measures. This relationship is discussed in more detail at the end of the account of *Isoetes*.

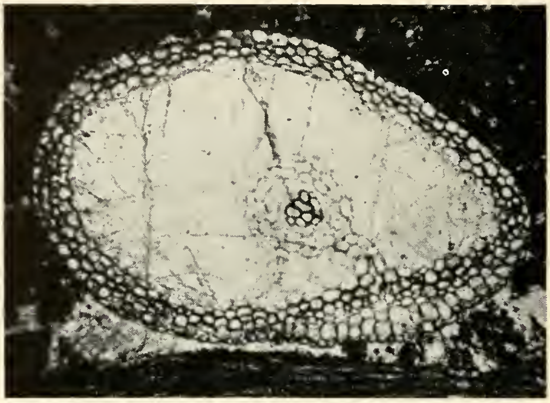

FIG. 608.—*Stigmaria ficoides.* Transverse section of root showing similarity of structure to the root of *Isoetes. Stigmaria* is a palaeozoic fossil.

ANATOMY OF THE LEAF

The leaf is from 2 to 6 in. long and comprises an expanded and thickened base, with an upper portion which is awl-shaped and sharply pointed. Every leaf seems to be potentially a sporophyll, as traces of abortive sporangia occur at the base even of the vegetative leaves. A similar condition is found in *Lycopodium selago,* which likewise has no specially organized strobili.

The leaf has no apical cell and growth is **intercalary,** from near the base, as in Monocotyledons. The upper part of the leaf shows, in transverse section, four large intercellular cavities or **lacunae** separated by parenchymatous diaphragms (Fig. 609), a condition which is usually found in submerged aquatic plants. In the centre runs a single, unbranched vascular

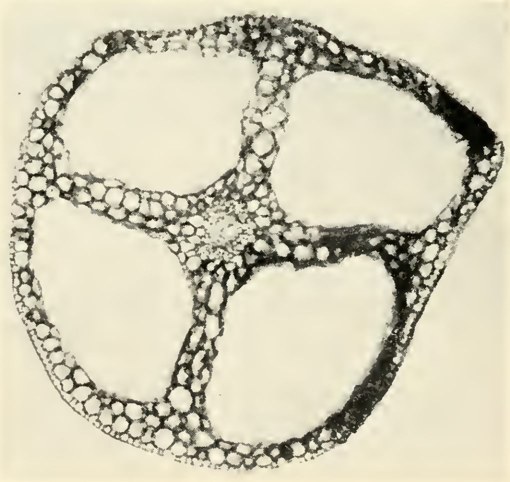

FIG. 609.—*Isoetes lacustris.* Transverse section of the leaf showing the central vascular strand and large intercellular cavities.

bundle. In the lower part of the leaf this has a collateral structure, with an arc of thick-walled phloem on the outer (abaxial) side, and a very reduced xylem consisting of one strand of protoxylem elements and a few small metaxylem tracheids. These latter lie on both the inner and outer sides of the protoxylem, which is therefore **mesarch.** Further up the leaf the xylem becomes **exarch** and the protoxylem strand is replaced by a cavity in which traces of lignified walls remain. Often the metaxylem tracheids are also resorbed in the same way, only cavities marking their position. The phloem has sieve tubes in some species, but none have been observed in *Isoetes lacustris.*

At each side of the bundle in the expanded leaf base may be seen a narrow cavity containing mucilage and partly disorganized cells. This is of unknown significance, but it is interesting to notice that exactly similar cavities flank the leaf trace in the fossil plant *Lepidodendron*, where they are called **parichnoi.**

The leaf base has two colourless wings, which extend a considerable way round the circumference of the stem. Between them lies a cavity in the leaf tissue, the **fovea,** opening to the ventral (adaxial) side, and containing a sporangium * (Fig. 610).

The opening of the fovea is partially covered by a membrane growing downwards from above, called the **velum.** Immediately above the fovea is the heart-shaped **ligule.** This is much larger and more complex than in *Selaginella*, though it grows from a single cell. It arises from a cavity in the leaf tissue, the **ligular pit,** and consists of four portions, firstly a sheath of glandular-looking cells, in contact with

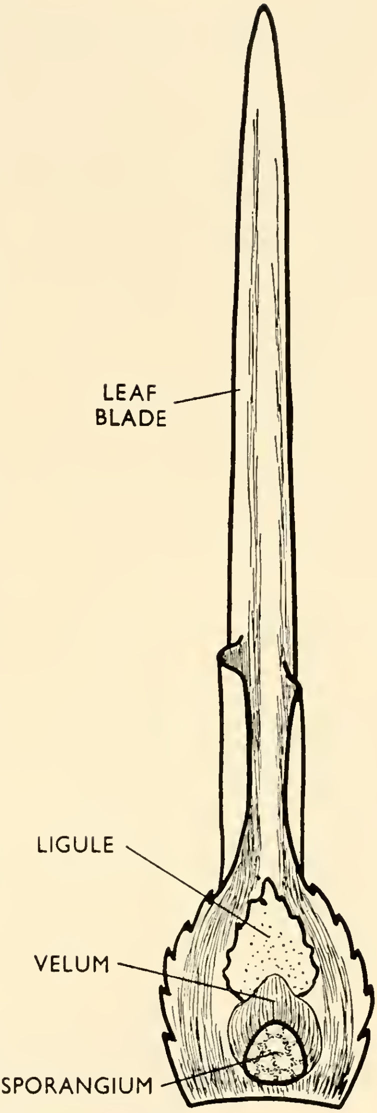

FIG. 610.—*Isoetes lacustris.* A single sporophyll viewed from the adaxial side showing the ligule and a sporangium in the sporangial cavity. (*After Troll.*)

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* A remarkable peculiarity, found only in the specimens from a single lake in the Vosges Mountains, is the development of detachable vegetative buds, or **gemmae** from the inner side of the leaf base, just below the position of the sporangia. The latter are completely abortive and this particular variety relies solely on vegetative propagation, like certain viviparous Flowering Plants.

the leaf tissue ; secondly the **glossopodium,** a rounded mass of large empty-looking cells ; thirdly the ligule proper which turns upwards and lies close against the leaf surface, and lastly an apex of dead cells. In the tissue of the leaf around the lower part of the ligule there lies a zone of short tracheids, not connected to the leaf bundle, which may be compared to the **transfusion tissue** of the leaves of Gymnosperms (see p. 673).

It is notable that the ligule appears very early in the development of the leaf rudiment and grows much more rapidly, overtopping and curling over the apex of the leaf itself. Its cells appear at this stage to be secretory, as they have very large vacuoles and there is no surface cuticle. It is probable that it secretes mucilage to moisten the stem apex and the young leaves. If so, this function is soon outgrown, and in the mature leaf it has been left so far behind in growth that it seems to be only a functionless vestige, devoid of chlorophyll or starch. It does not, however, wither away, as in *Selaginella*. The lower portion of the ligule is partially covered by an upward flap of leaf tissue—the **labium.** Both this and the velum develop from cells immediately above the young sporangium and are not sterilized sporogenous tissue as has been stated.

DEVELOPMENT OF THE MEGASPORANGIUM

The megasporangium is very large, about 5 mm. long by 3 mm. broad. The cells are at first all alike, but at an early stage certain cells increase in size and are recognizable as the **spore mother cells,** while the cells of the surrounding tissue continue to divide and grow. This differentiation of spore mother cells in the midst of a parenchymatous tissue recalls strikingly the growth of an embryo sac in the nucellus of the Seed Plants, and the resemblance is increased by the enclosure of the sporangium within an integument of leaf tissue. Eventually certain of the mother cells outgrow the others and each divides to produce four **megaspores** (Fig. 611).

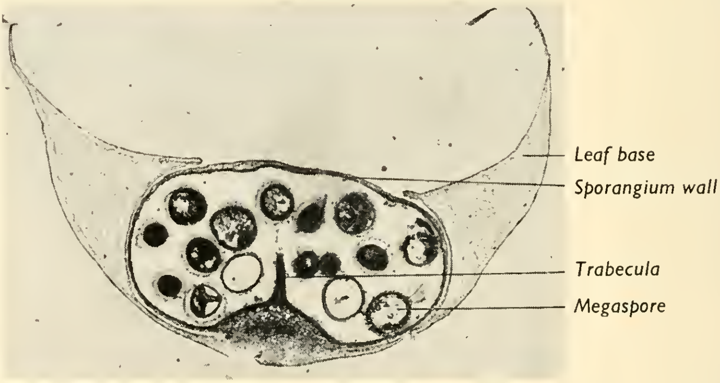

FIG. 611.—*Isoetes lacustris.* Transverse section of megasporophyll passing through the megasporangium.

Before the division of each mother cell the included starch grains arrange themselves into four groups, and the four nuclei resulting from the meiotic divisions place themselves in contact with the four starch groups. This is immediately followed by the formation of new dividing walls.

The first wall to form round the megaspore is a membrane which later becomes the **perispore.** Within this is secreted the **exospore,** which later divides into three layers, the inner two being the **mesospore** and the **endospore** respectively. This recalls the megaspore of *Selaginella*, and in the present plant there is the same separation of the protoplast from the wall during development, which occurs in the former type. The number of megaspores in each sporangium varies but is of the order of 100 to 200.

Among the cells of the archesporium in its early stages there are four distinct conditions. Firstly there are the true spore mother cells. Secondly there are cells which enlarge, like the former, but remain sterile and subsequently divide. Thirdly there are the cells which form the **tapetum,** arranged in three or four layers round the mother cells. Lastly there are rows of cells which remain small and comparatively empty. These last persist in the ripe sporangium as membranes running across the sporangium among the mature spores, and called the **trabeculae.** All these kinds of cells are apparently potentially sporogenous and have been altered by progressive sterilization.

The trabeculae apparently represent a development of the processes which arise from the sub-archesporial tissue in the sporangium of *Lycopodium,* and they have several parallels in the sporangia of species of *Lepidodendron.* Their function is apparently nutritive like that of the tapetum.

The mature spores are covered by a dense white perispore, very warty on the surface and marked with a prominent triradiate ridge which determines the lines of dehiscence.

The sporangial wall is usually two to three cells thick and does not dehisce but liberates the spores by decay.

Development of the Microsporangium

The **microsporangium** is at first identical in structure with the megasporangium. The massive archesporium and the sporangial wall are not clearly segregated until a late stage of development. Before the mother cell stage is reached there is an evident differentiation of trabeculae, the cells of which lose most of their protoplasm (Fig. 612). These trabeculae partially divide the archesporial mass into a number of portions, each of which is surrounded by a tapetum, two or three cells thick. The mass of sporogenous cells is very large and the number of **microspores** is probably the largest formed in the sporangia of any vascular plant. It is estimated to be as high as half a million in the present species, while some other species may have twice that number. As in the megasporangium, there is no dehiscence of the sporangial wall.

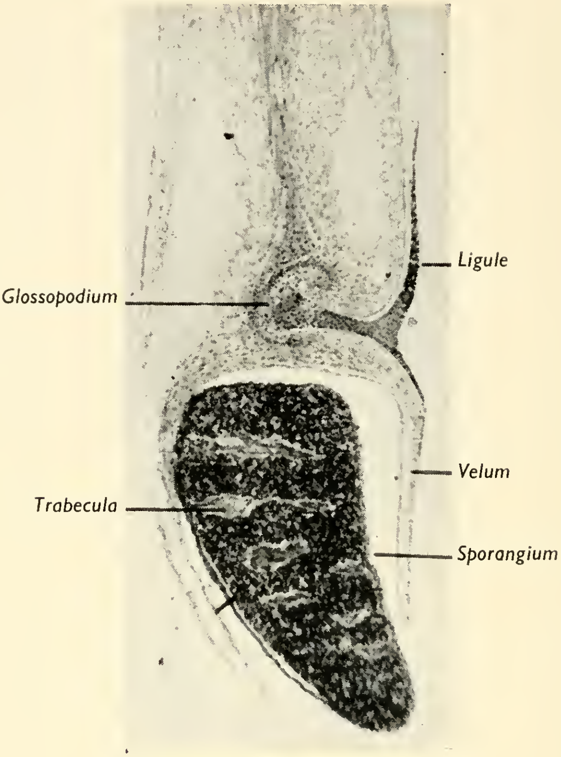

Fig. 612.—*Isoetes lacustris*. Longitudinal section of microsporophyll showing the structure of the ligule and microsporangium with trabeculae.

The Male Gametophyte

The microspores are bean-shaped with smooth walls. They do not begin germination until after they are set free, but they do so most promptly, though rather irregularly, in winter, when the male prothallus ripens in about two weeks from shedding. This is probably the natural time at which the sporangium decays. In the first place a small **prothallial cell** is cut off at one end of the spore, the rest of the spore forming the **antheridium** (Fig. 613). Obliquely intersecting walls divide it into four peripheral cells and four central ones, each of the latter forming a single-coiled **antherozoid,** which, like those of the Ferns, and unlike those of Lycopodiales, has a tuft of fifteen flagella (Fig. 614). The peripheral cell walls dissolve, leaving the antherozoids free inside the spore. They are liberated by the eventual dehiscence of the spore wall along the triradiate ridge.

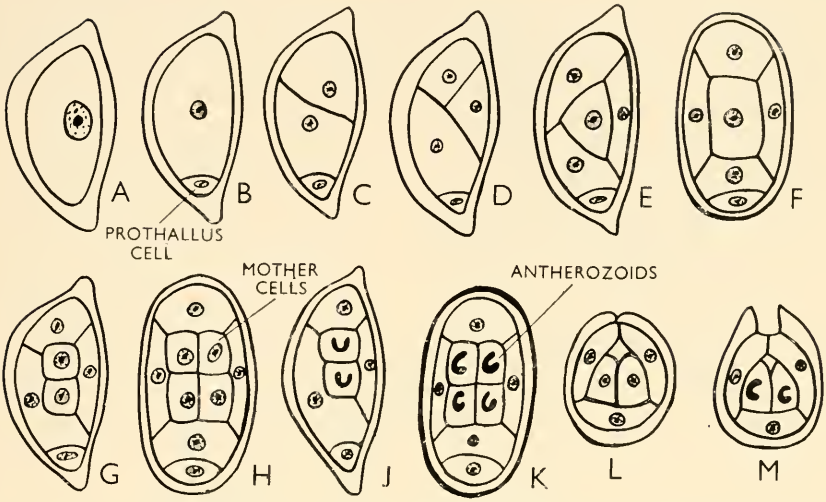

FIG. 613.—*Isoetes lacustris.* Development of the male gametophyte showing differentiation of prothallus cell and antheridial cell, the latter forming a wall and antherozoid mother cells. Note that the prothallial cell does not disorganize as in *Selaginella.* (*From Smith after Liebig.*)

THE FEMALE GAMETOPHYTE

The megaspores are nearly globular, but the three converging ridges on one side are very prominent and form the angles of a flattened pyramid. It is along these ridges that the spore dehisces.

At the time of shedding the protoplasm fills the whole cavity of the spore, and at no time is there a large central vacuole, as there is in *Selaginella.* There are large numbers of both oil drops and starch grains present.

The primary spore nucleus lies at the apex of the protoplast, and its first divisions are free, without any cell-wall formation. This continues till about fifty nuclei have been formed, most of which are congregated at the apical end with only a few elsewhere. Cell-wall formation then begins simultaneously right across the spore apex. It starts with the formation of incompletely enclosed areolae, which are subsequently closed by end walls. Cell formation spreads along the periphery towards the base of the spore, and only finally is the central mass divided up into uninucleate cells (Fig. 615). The spore wall now opens from the apex along the ridges, disclosing the cellular surface of the prothallus. Only one **archegonium** is at first produced, and if this is fertilized no other appears, but if fertilization fails a succession of archegonia, up to twenty or thirty, may be formed. The archegonium is developed from one superficial cell, which enlarges at an early stage. This divides horizontally into two, the upper of which forms a four-tiered neck ; the lower cell again divides into a single canal cell, below the neck, and a lowermost cell which itself divides to form the ventral canal cell, on top, and the **oosphere** below. The neck scarcely rises above the prothallus surface.

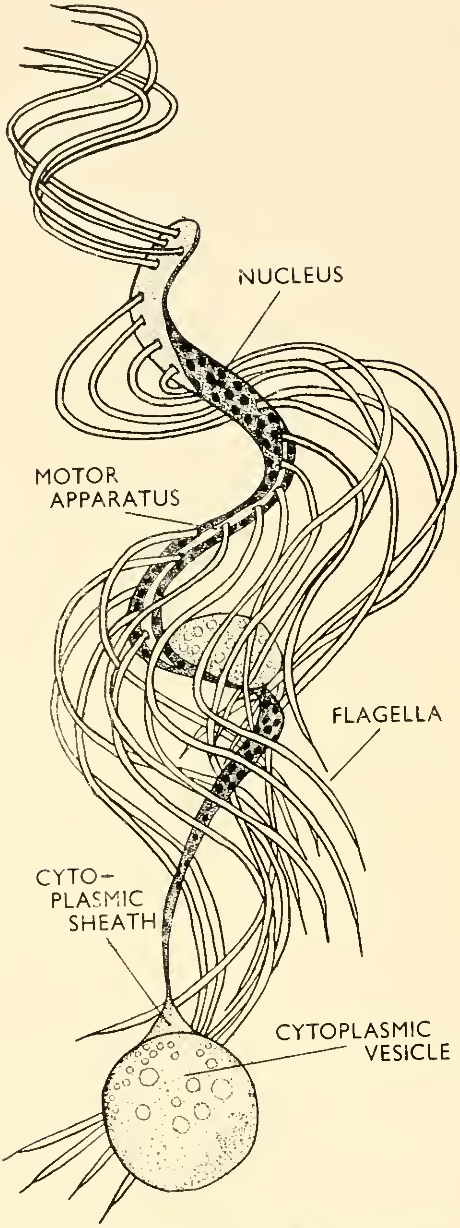

Fig. 614.—*Isoetes lacustris.* Mature antherozoid. (*After Dracinschi.*)

Development of the Embryo

The first division of the fertilized oosphere is more or less inclined to the horizontal. The embryo is at first globular and has no suspensor. The upper portion produces the **foot** and the lower portion the **cotyledon** and the

root, but there is apparently a rotation during development so that the foot comes to lie beneath, while the root-cotyledon axis lies horizontally above (Fig. 616). At this stage the ligule of the cotyledon begins to grow from a single large cell and is about half as long as the cotyledon by the time the

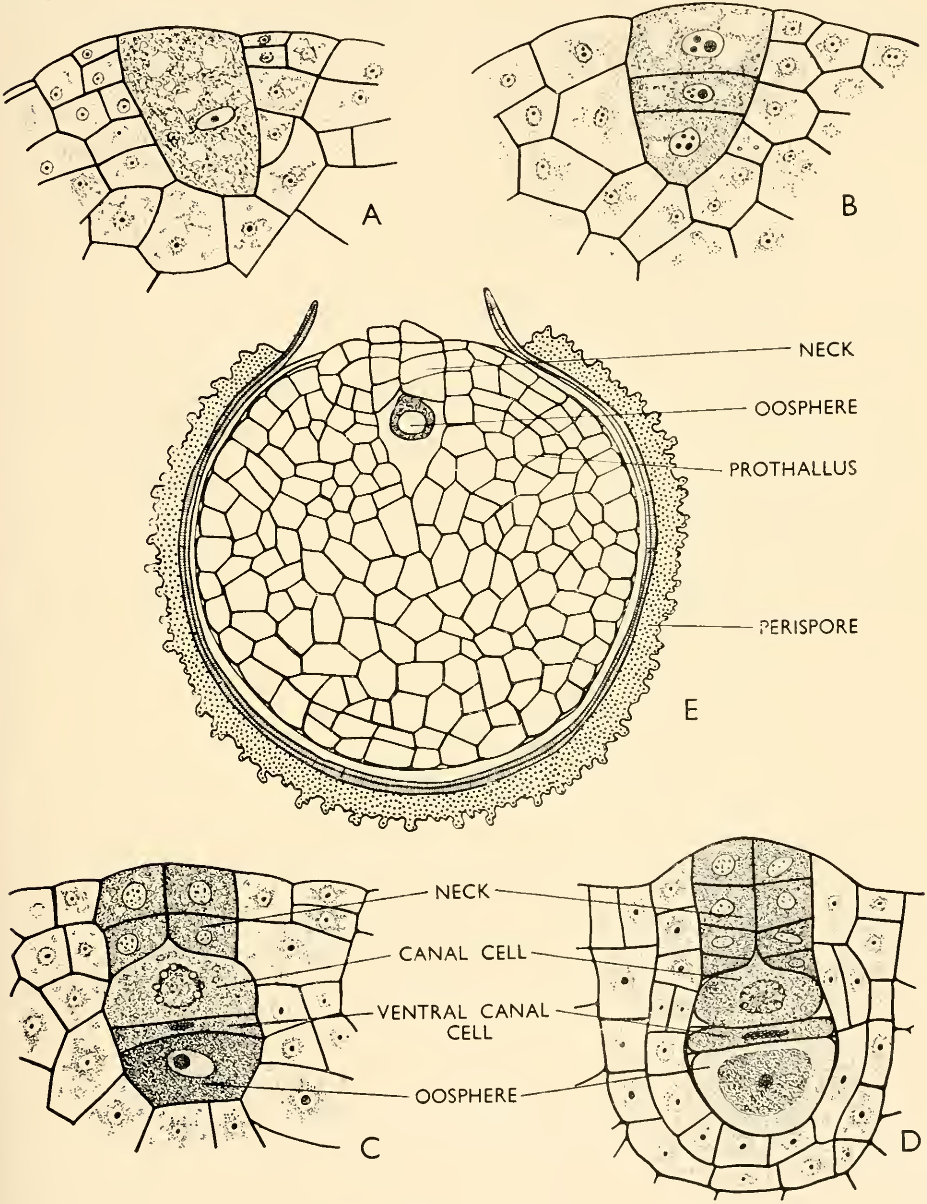

Fig. 615.—*Isoetes echinospora.* Development of female gametophyte and archegonium. A, Mother cell of archegonium. B, Separation of neck cell, canal cell and oosphere mother cell. C, Further differentiation of neck cells and ventral canal cell. D, Mature archegonium. E, Section through the megaspore containing the mature female prothallus with archegonium. (*After Campbell.*)

latter breaks out from the prothallus. Up to this stage there has been no stem apex, but a scale called the **cotyledonary sheath** makes its appearance at the base of the cotyledon, and between them is formed the meristematic group which becomes the apical tissue of the stem. The stem is, however, for long very ill-defined, and the apex is only recognizable as such because it is from this region that all the leaves after the cotyledon are produced.

The foot increases in size by absorption of all the remainder of the prothallus until it fills the spore cavity. The cotyledon and the first root grow out, at first horizontally, and the prothallial tissue, which expands with their growth, encloses each in a sheath, which is eventually ruptured. The cotyledon, which resembles anatomically the other leaves, then turns upwards and the root downwards (Fig. 616).

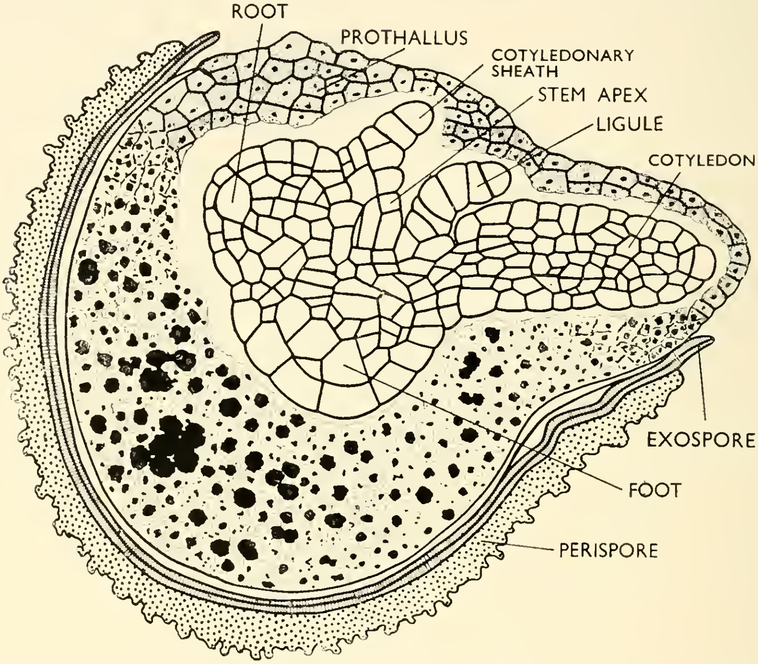

Fig. 616.—*Isoetes lacustris.* Section through megaspore and female prothallus showing developing embryo and disorganising prothallial tissue. (*After Liebig.*)

Relationships

The affinities of the other Vascular Crytogams which we have discussed are in most cases fairly clear, but the unique characteristics of *Isoetes* make it a more difficult problem. Except for the Filicinean antherozoid, however, the bulk of the characters, such as the simple leaf with its one leaf bundle and ligule, the sporangia borne on the adaxial leaf surface, the spores, and especially the gametophytes and the embryology strongly suggests a relationship to the Lycopodiales.

The presence of a parichnos in the leaf base and the anatomy of the root are not characters of any living Lycopod, but are both found in the fossil Lepidodendraceae. In this group it is the tall, unbranched or sparsely branched *Sigillaria* which seems to be the nearest type. Now *Sigillaria* was the only Lepidodendroid to survive beyond the Carboniferous Period, and it had a successor in the Mesozoic Period called *Pleuromeia*, which retained the outward morphology of *Sigillaria* with two very significant differences. It became progressively shorter, so that instead of a 50-foot tree it formed a plant only 2 or 3 ft. high, and the extensive Stigmarian rhizophore system of *Sigillaria* was reduced to four, blunt, upturned lobes at the stem base, on which the roots were produced. (See " Palaeobotany " in Volume III.)

In *Isoetes* the reduction of this rhizophore system has gone still further, so that it no longer shows externally and is preserved only in the upturned rhizophore-lobes at the base of the stele. Nevertheless the phylogenetic connection is highly probable.

It has been suggested that *Pleuromeia* represents a Sigillarian type adapted to life in isolated marshes during the desert period of the Trias and *Isoetes* suggests a further stage of reduction in adaptation to a wholly aquatic life. The morphology of *Isoetes* indicates just such a reduction from a taller stock by telescoping. In the Cretaceous Period there occurred another plant, *Nathorstiana*, which only reached a foot in height. It shows an even greater resemblance to *Isoetes*, although the rhizophores are still externally recognizable as lobes at the stem base. As Walton says, " There seems little doubt that the arborescent Lycopods of the Palaeozoic, and *Pleuromeia*, *Nathorstiana* and *Isoetes* form a series in which there is a progressive reduction in size and in which the root-bearing region becomes simplified in external form."

PSILOPSIDA

The Psilopsida are Pteridophyta in which there are no true roots. The organization is of a simple type, the branching being usually dichotomous. Leaves are either absent or very much reduced. The plants are always homosporous, the sporangia are terminal and are not aggregated into strobili. The prothalli, where known, are saprophytic and subterranean.

The series is divided into two orders, the Psilotales, which are living plants, represented by the two genera *Psilotum* and *Tmesipteris*, and the Psilophytales, an order of archaic fossil plants which will be dealt with in Volume III.

Psilotales

This is a very small order, of limited distribution, but interesting because of its apparent connection with one of the oldest known groups of extinct land plants, the Psilophytales, which flourished in Devonian times, some 1,500,000,000 years ago.

There are only two genera, both small plants of peculiar morphology and saprophytic habit: *Tmesipteris*, which is limited to Australasia and the East Indies, and *Psilotum*, which is fairly common generally in the Tropics and

Sub-tropics. Though somewhat different in their habit they are sufficiently related to form only one family, the Psilotaceae. The shoots of *Tmesipteris* are unbranched and leafy (Fig. 617), while those of *Psilotum* branch dichotomously and have only scale-leaves. We shall describe as a type *Psilotum triquetrum*.

FIG. 617.—*Tmesipteris tannensis*. Plant growing epiphytically on the stem of a Tree Fern.

Psilotum triquetrum

This is the principal species, the only other one, *P. complanatum*, which is much rarer, differing chiefly in its flattened stem.

The plant is slender and shrubby, rarely as much as a metre in height, with green, ridged, dichotomous stems (Fig. 618). Superficially it is not unlike a leafless plant of the Whortleberry, *Vaccinium myrtillus*. It grows in humus pockets, usually on the stems of Palms or Tree Ferns, but also in rock clefts, and often hangs downwards. The stems are perennial and somewhat xerophytic in structure.

At its base the stem merges into a slender, dichotomous **rhizome,** which is clothed with brown rhizoids, except at the apices, which are naked and white. There are no roots and the rhizome forms no leaves. The rhizome lives for several years underground, forking frequently and irregularly until it forms a coralloid mass (Fig. 619). All this time it is saprophytic and its cortex shelters a mycorrhizal Fungus. At length it sends out almost naked branches which turn upwards to the light and grow into the first green shoots, which, although initially weak and small, get larger with successive years until at length the fruiting stage is reached.

FIG. 618.—*Psilotum triquetrum.* Plants growing epiphytically on the trunk of a Palm.

These aerial shoots, which at the base are round and brown, like the rhizome, become green and three-angled in their upper parts. Both rhizome and green shoot grow by means of three-sided apical cells and that of the shoot produces minute, bifid, scale-leaves, placed at first in three vertical rows, an arrangement which is lost in the older parts.

The upper leaves bear, apparently in their axils, short pedicels, on each of which is a triad of closely united sporangia, which are homosporous and measure 2 to 3 mm. across. The two cusps of the bifid leaf clasp the base of the sporangium closely (Fig. 620).

The morphology of this structure is obscure and has been variously explained. The opinions held may be reduced to two. Firstly, that the whole structure is a bifid sporophyll, bearing a synangium or plurilocular sporangium, a view which tends to bring the plant into line with *Lycopodium*. Secondly, that the whole sporangium-bearing structure is a short fertile axis, a **sporangiophore,** terminating in a synangium and bearing two leaves or bracts. If the latter be the case these sporangiophores are not lateral branches in the usual sense, since they have no subtending leaf and they must therefore be regarded as reduced limbs of successive apical dichotomies of the main axis.

Fig. 619.—*Psilotum triquetrum.* Complete plant showing branched rhizome and shoots bearing sporangia. Much reduced.

Fig. 620.—*Psilotum triquetrum.* Portion of a branch bearing synangia. Below the middle synangium may be seen the two cusps of the bifid leaf.

Although the first view is the simpler the objections to it are twofold. Nowhere else is there a case of a sporophyll bearing a synangium on its adaxial face. Secondly the so-called sporophyll receives no vascular trace from the stem while the synangium does, a fact which speaks strongly for its axial nature. Comparison with *Tmesipteris* helps to confirm the sporangiophoric theory, which may be accepted as the more probable (Fig. 621). If it be accepted it falls into line with the ancient Psilophytales in which one branch of each dichotomy of the axis is fertile with a terminal sporangium, while the other remains sterile. The trilocular condition in the sporangium of *Psilotum* is interpreted as due to a primary dichotomy of the sporangiophore, one limb of which develops a sporangium, while the other again divides, each end forming immediately another sporangium. Abnormal cases are known in which this branching may be seen fully developed.

FIG. 621.—*Tmesipteris tannensis.* Fertile shoot showing synangia attached to bifid leaves.

ANATOMY OF THE STEM

The stem and the rhizome both grow from three-sided apical cells. Both branch by dichotomy and the apex of the stem cuts off, additionally, three rows of leaf initials from its three faces. In the early stages the sterile leaves and the sporangiophore shoots are alike, and in the latter case the synangium appears as a hump of tissue on the adaxial face of the initial only after it has reached about half its full size.

In section the stem shows a strongly cutinized epidermis with stomata in the grooves of the surface (Fig. 622). The cortex develops three zones. The outermost consists of cells which appear rectangular in cross-section, but which are very irregular in outline when seen longitudinally, with air spaces between them. This is an assimilatory tissue and contains abundant

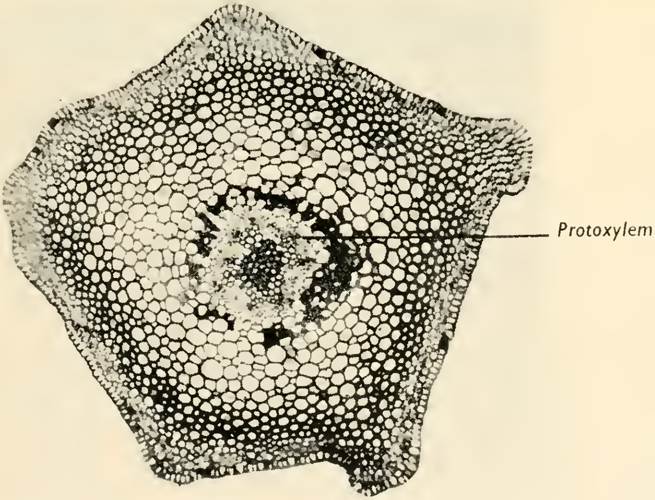

FIG. 622.—*Psilotum triquetrum.* Transverse section of aerial stem showing thickened cortex and stele with central core of sclerenchyma and several external protoxylems.

chloroplasts. Similar cells form the central tissue of the leaf. Inside the assimilating layer is a broad band of sclerotic cells and within these again lies a zone of thin-walled parenchyma.

The endodermis round the stele is well marked. In the centre of the stele is a core of sclerenchyma cells, round which lies a narrow band of scalariform xylem elements, with the spirally thickened protoxylems projecting outwards as radial ribs. This is a siphonostelic type of structure, though the pith is sclerenchymatous, not parenchymatous, as is usual in Ferns. The phloem is of very indefinite character. Tubular cells are present, but they have not the structure of sieve tubes and are called by the non-committal name of **leptoids.** In addition this zone contains groups of cells with their walls thickened, especially at the angles. These cell groups lie opposite the xylem-ribs, but their nature is unknown. In the upper part of the stem the central group of sclerenchyma is not formed and there are no xylem ribs, so that the structure here is typically protostelic.

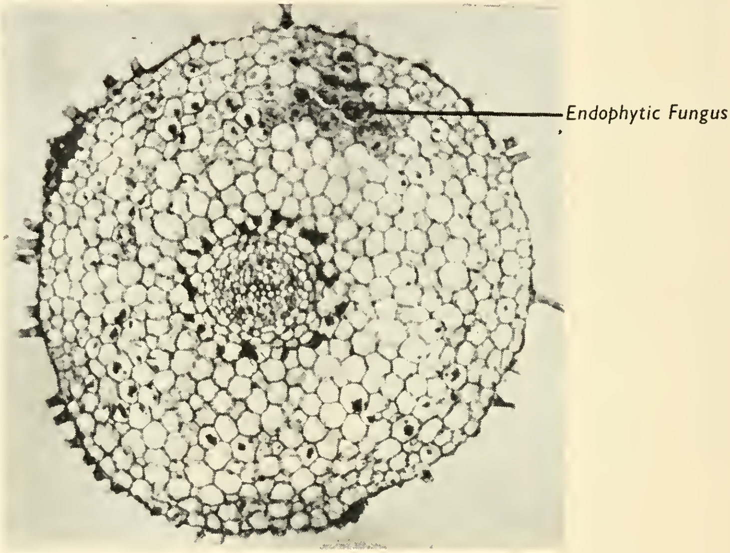

FIG. 623.—*Psilotum triquetrum.* Transverse section of rhizome with mycorrhizal cortex and small stele with central xylem group.

The traces which go to the sporangiophores consist of spiral elements given off from the protoxylems ; although small they show a distinct mesarch structure. As mentioned above the leaves receive no vascular tissue. Only the branch traces make any gap in the xylem ring.

The stele of the rhizome has no pith and the xylem mass is usually rounded in outline, often lacking any protoxylem or ribs (Fig. 623). There is very little phloem and the endodermis is normal. Outside the endodermis are three or four layers of thick, brown-walled cells, as in a Fern root, while the bulk of the cortex is thin-walled and mycorrhizal. All the cells of the surface layer extend into two-celled **rhizoids.** In starved conditions the upper cell of many of the rhizoids divides and produces a small nodular **gemma,** which on being detached develops into a new rhizome.

At the extreme base of the stem the stele is protostelic, as in the rhizome, but the xylem is often surrounded by scattered secondary tracheids, apparently relics of ancestral secondary thickening. No cambium is, however, formed. At this level the stele resembles that of the fossil *Sphenophyllum*, but a little higher up a parenchymatous pith appears, which still higher gives place to the typical central sclerenchyma, and thus the resemblance is lost in the mature stem.

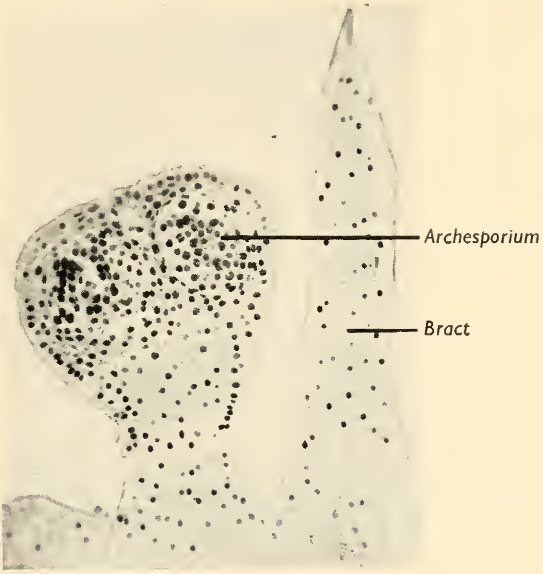

Fig. 624.—*Psilotum triquetrum.* Longitudinal section of a synangium showing two groups of archesporium and sporangiophore.

Development of the Sporangium

It has been for some time an open question whether we had here to deal with a true synangium, of united sporangia, or with a single trilocular sporangium. The earliest stages of development show, however, that each loculus arises separately from a single epidermal cell of the sporangiophore. We may therefore assume that the structure is a union of three sporangia, that is, a true **synangium.** The first division of the primary cell is periclinal and separates a **jacket cell,** from which a wall three to five cells thick develops, and one **archesporial cell** which produces a central mass of sporogenous cells (Fig. 624). The three sporangia are grouped around a central sterile tissue, the sporangiophore axis, into which the trace bundle from the stem runs up and ends blindly.

When the sporangia are nearly full grown, small groups of cells in the middle of the archesporium begin to divide repeatedly, while all the rest of the cells disintegrate into a plasmodial mass, by means of which the spores, developing from the central cells, are nourished. There is no true tapetum formed. The spores are bean-shaped with finely reticulated walls. Meanwhile the sporangial wall cells have thickened considerably, except along one vertical line running from the apex to base of each sporangium. These are the lines of dehiscence, along which the entire structure opens into three segments releasing the spores (Fig. 625).

Development of the Gametophyte

The spore wall opens along a dehiscence-cleft in one side, and reveals a single, thin-walled cell, which by oblique divisions establishes an apical cell, by whose activity a cellular body is formed. This elongates into a cylindrical, slightly branched prothallus, covered with brown rhizoids and growing by means of an apical meristem (Fig. 626). It closely resembles a portion of the rhizome. The tissue is colourless, saprophytic and mycorrhizal, as in the rhizome, but there is normally no vascular tissue, though cases are on record in which tracheids were found (Fig. 627) in large prothalli, forming a discontinuous strand.

Antheridia appear first, each developing from a superficial cell, and they are spherical structures with a single-layered wall. The antherozoids are spiral and multiflagellate, like those of *Isoetes* and the Ferns.

The archegonia develop as usual from a superficial cell which divides periclinally. The outer cell forms a neck four to six cells in length. The development of the inner cell is uncertain, but it probably forms an oosphere, a ventral canal cell and two neck canal cells. When the archegonium is mature the neck breaks off, leaving only the lowermost one or two tiers of cells and thus opening the neck canal to the antherozoids.

Development of the Embryo

Embryonic development is very simple (Fig. 628). The oospore divides periclinally and the upper cell develops into the axis, the lower cell into a foot, which sends out finger-like processes into the prothallial tissues. There is a marked line of division between axis and foot, and when the developing axis has broken through the surface of the prothallial tissue the foot and the axis separate, the foot remaining attached to the prothallus. The embryonic axis elongates vertically, before it becomes free, and develops either one or two apical cells. In the latter case the axis is dichotomous from the start, but in any case a first dichotomy soon occurs. The prothallus tissue grows up like a calyptra round the young axis, but the growth activity of the embryo soon breaks through this. When the axis is cut off from the

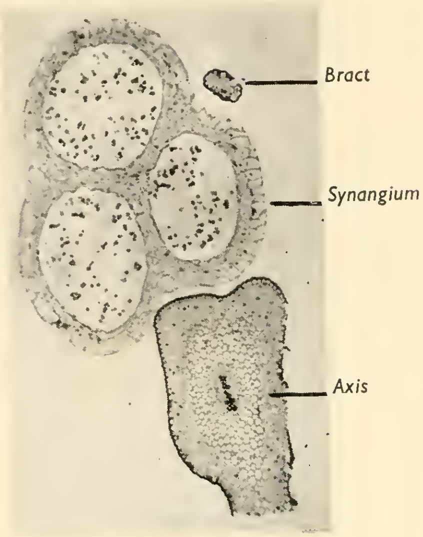

FIG. 625.—*Psilotum triquetrum.* Transverse section of a synangium showing three united sporangia with thick walls.

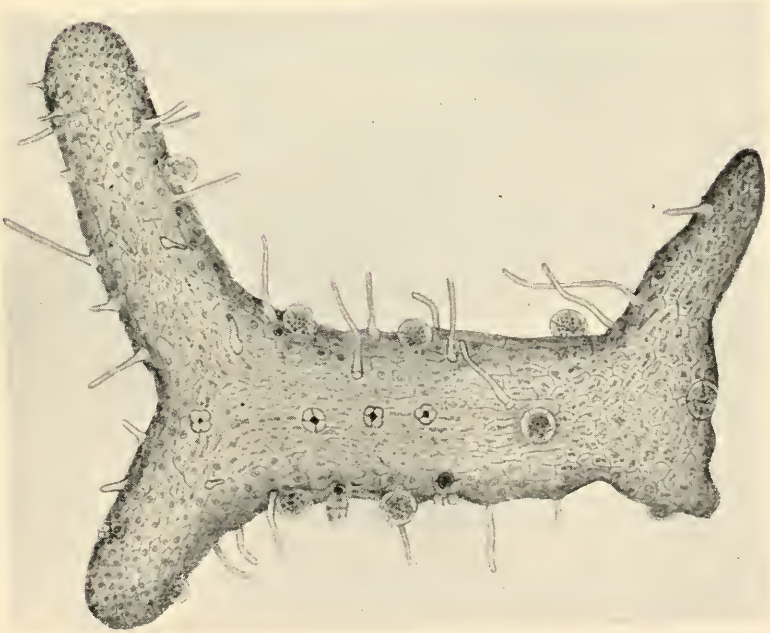

FIG. 626.—*Psilotum triquetrum.* Prothallus with rhizoids, antheridia and archegonia. Enlarged about ten times. (*From Zimmermann, "Die Phylogenie der Pflanzen."*)

foot it develops rhizoids externally and a vascular stele and mycorrhizal cells internally, and thus begins a new rhizome, which continues to branch either dichotomously or by the formation of adventitious side branches.

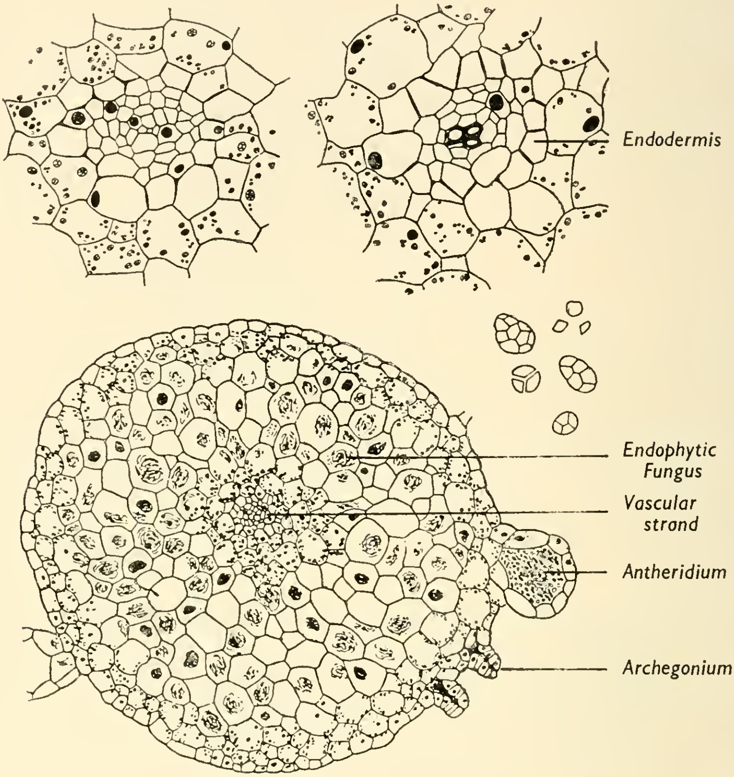

FIG. 627.—*Psilotum triquetrum.* Sections of the prothallus showing development of vascular tissue. (*After Holloway.*)

Psilotum possesses a collection of primitive characters without a parallel among living Pteridophyta and clearly indicating a relationship to the ancient Psilophytales. They may be summarized as follows :—

1. The predominance of dichotomy.
2. The absence of roots.
3. Protostelic structure of the rhizome.
4. Mesarch sporangiophore traces.
5. Terminal sporangia.
6. Homospory.
7. Thick sporangial walls.
8. Close similarity of both generations.

This last point is not without significance in regard to the origin of the alternation of generations, when we consider the primitive status of the plant, and its relationship to one of the most ancient groups of Vascular Cryptogams.

Among the Thallophyta there are many examples of homomorphic alternation (see p. 182), but in the living Bryophyta, Pteridophyta and Spermatophyta heteromorphic alternation is the rule, and with advancing evolution the difference between the two generations has steadily increased. In *Psilotum*, on the other hand, the prothallus almost exactly resembles the sporophytic rhizome in structure.

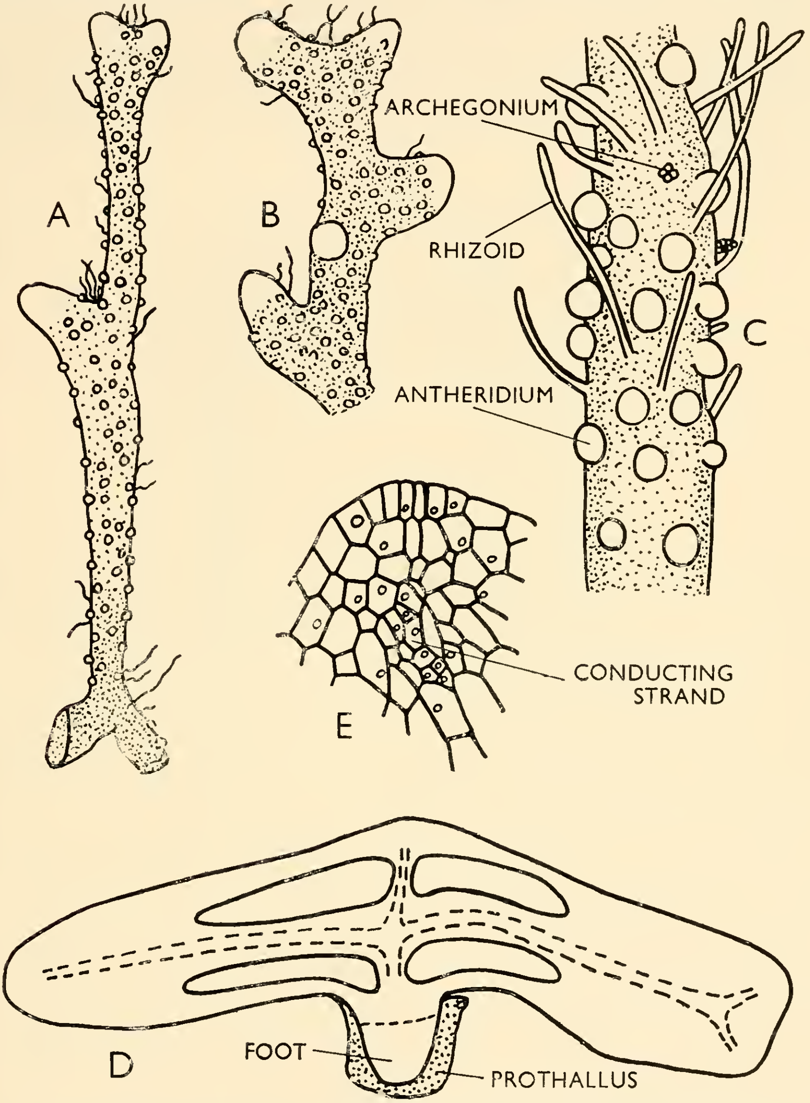

Fig. 628.—*Psilotum triquetrum.* Prothallus and embryo. A and B, Portions of a prothalli covered with antheridia. C, Portion of prothallus enlarged, showing antheridia and archegonia. D, A young sporeling showing three apices, conducting strands and distribution of the Fungus outlined. The foot is still embedded in the prothallus. E, One of the apices of D showing late origin of the conducting strand. (*After Holloway.*)

SPHENOPSIDA

This series of the Pteridophyta is marked by the very slight development or absence of branching in the main axes and by the clearly jointed stems on which microphyllous leaves and lateral branches are borne in whorls. The members are all homosporous with stalked sporangia which are aggregated into strobili. The gametophytes of the living types are sub-aerial and green. The jointed character of the stems has led to their being named the **Articulatae** by many authors.

The Sphenopsida include the following two orders :—

1. **Equisetales.**

    Equisetaceae : Living plants belonging to the single genus *Equisetum.*

    Calamitaceae : Carboniferous fossils.

2. **Sphenophyllales.**

    Sphenophyllaceae : Carboniferous fossils.

EQUISETALES

The Equisetales are Pteridophyta which are characterized by hollow, jointed stems, with very small, simple leaves, arranged in whorls. The sporangia are borne in groups attached to a common stalk or sporangiophore, and these are arranged in whorls to form terminal cones or strobili.

The Calamitaceae were large forest trees which formed a dominant part of the vegetation in Palaeozoic times but became extinct at the close of that era. In structure they resemble very closely the Equisetaceae of the present day, and there can be little doubt that the living types of *Equisetum* are the direct decendants of this family.

There is a marked parallelism between the fossil Lepidodendrons and the present-day Lycopodiums on the one hand, and the Calamites and the living Equisetums on the other, for both groups have decreased in size in the course of evolution and their structures have become simplified, as for example in the absence of secondary thickening in the modern forms, which was well developed in the Carboniferous ancestral types. At that period the two fossil groups formed a major part of the vegetation, in so far as we know it, while the modern representatives are relatively inconspicuous plants.

We shall describe here one example of the order, *Equisetum arvense*, and return to a consideration of the fossil representatives in Volume III.

Equisetum arvense (The Field Horsetail)

There are several species of Horsetail which occur commonly in this country. *Equisetum arvense* (Fig. 629) is found in waste and gravelly places. In general habit the species show a strong resemblance to one another, all possessing a stiff, upright, jointed stem which bears **whorls** of poorly developed leaves, each whorl being united to form a sheath around the stem at each node. Sometimes the stem produces branches, and in such cases the branches themselves are developed in whorls, further intensifying the formal and geometrical appearance of the plant.

The **cones** are borne either at the apex of the main stem or of branches. In some species they develop at the apices of the ordinary vegetative stems, whilst in other species special, fertile, unbranched stems are produced which are devoid of chlorophyll. These are produced in the early part of the year and are followed later by the green stems.

FIG. 629.—*Equisetum arvense.* Two assimilating shoots and one fertile shoot with strobilus. Much reduced.

These vertical stems are connected underground to a branched rhizome which often penetrates into the ground to a considerable depth. In appearance this rhizome is somewhat similar to that of the vegetative stem except that large numbers of adventitious roots are formed at the nodes, arising usually from the bases of the lateral buds. Some branches of the rhizome remain short and develop into tubers, which will grow if detached and serve as a means of vegetative propagation.

The largest British species, *Equisetum telmateia*, may reach a height of some 6 to 8 ft., but most of the other species are smaller, rarely attaining a height of more than 2 ft.

Anatomy of the Stem

The characters of the stem are shown more clearly in the aerial shoots than in the underground rhizomes. There are two kinds of stems in *Equisetum arvense.* Firstly, the fertile shoots which appear in March and bear the reproductive organs. These stems are unbranched, pale brown in colour, contain no chlorophyll either in their leaf-sheaths or the stem itself, and die down as soon as the spores are shed. The second kind of stem is much branched and forms the vegetative system and, possessing chlorophyll, it serves as the assimilatory organ of the plant. The surface is ribbed lengthwise, and the ribs alternate regularly in successive internodes. The lateral branches arise from buds on the stem at the nodes, inside the leaf-sheaths. They are equal in number to the leaves of the node at which they arise and alternate with them. As the buds develop they break through at the base of the leaf-sheath so that they appear to come from beneath it. The initial cell of the bud divides into an upper, or epibasal, and a lower, or hypobasal half, and the subsequent divisions of these two cells follow the same plan as in the development of the embryo. The branch is organized from the epibasal and a root from the hypobasal portion, though in the aerial stem it usually remains dormant. It is a simple and primitive type of shoot organisation, based on a single axis, as in the gametophytes of the Musci.

The internal anatomy of the stem is relatively simple and the vascular tissues are only poorly developed. The leaf trace bundles are arranged in a single circle, one entering from each leaf and passing straight down through the whole length of the internode until it reaches the node below, where it forks into two and joins with two bundles coming up from the internode below. It follows, therefore, that every internode contains a ring of as many bundles as there are leaves at the node above, and as the leaves alternate with each other at successive nodes, so also do the bundles in the corresponding internodes. Each ridge on the surface of the stem corresponds to the position of a vascular bundle, therefore the ridges also alternate.

In a transverse section through the stem we find that on the outside there is a strong epidermis with stomata in the grooves (Fig. 630). These stomata are peculiar in that the guard cells are completely covered externally by a pair of subsidiary cells, so that a double set of guard cells, one above the other, appears to be present. The cells of the epidermis are also remarkable for their strongly silicified outer walls, which accounts for the extremely hard texture of the stems of these plants, and earned for them their old name of " scouring rushes."

The cortex contains a variety of tissues. On the periphery, below the ridges, are longitudinal ribs of sclerenchyma which give the stem mechanical strength, the stelar xylem being poorly developed. Alternating with these, and therefore below the grooves on the surface, are bands of assimilating tissue containing chlorophyll, which take the place, physiologically, of the much-reduced leaves. The inner cortex is parenchymatous and contains a series of large intercellular cavities, forming, no doubt, an aerating system. These are called the **vallecular canals,** as each lies directly below a stem groove and therefore close beneath the assimilating tissue.

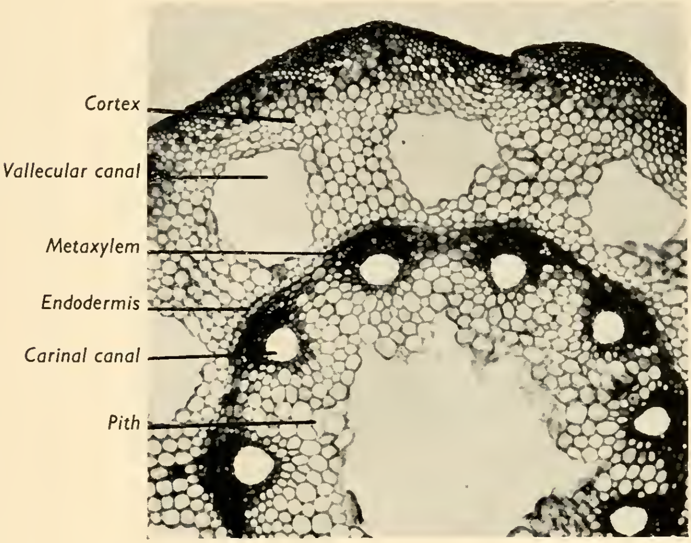

FIG. 630.—*Equisetum arvense.* Transverse section of the stem showing canals and vascular strands.

The cortex is bounded on the inside by an endodermis with well-marked Casparian bands on its radial walls, and within it lies the pericycle, forming the external layer of the stele. The stele itself consists of a single ring of vascular bundles, surrounding the large central cavity of the stem. This cavity occupies the position of the pith, which is present in the youngest internodes but soon breaks down leaving an empty space.

The general distribution of tissues in the rhizome is similar to that in the aerial stem, but the cortex is simpler, without any assimilatory tissue. There is an outer layer of dark-coloured sclerotic cells (Fig. 631).

The vascular bundles in the ring are widely separated by broad bands of parenchyma. Each bundle is **collateral,** that is, it has the xylem on the inner and the phloem on the outer side. The xylem has the shape of a " V," with the point, which consists of protoxylem, inwards (Fig. 632). This point is marked by another intercellular canal, the **carinal canal,** so called because it lies directly under one of the external ridges of the stem. The protoxylem elements are few and small and adhere loosely to the sides of this canal. The metaxylem forms the two limbs of the " V," but the two groups of cells composing it are separated from the protoxylem by several cells of xylem parenchyma. The phloem lies between the limbs of the xylem and is composed of phloem parenchyma and sieve tubes, with sieve plates on their oblique, transverse walls.

The separation of protoxylem and metaxylem is more than merely topographical ; they are also functionally distinct, and this renders any direct comparison with the vascular bundles in Spermatophyta impossible. In the latter group the bundles are common to both stem and leaf, that is, every

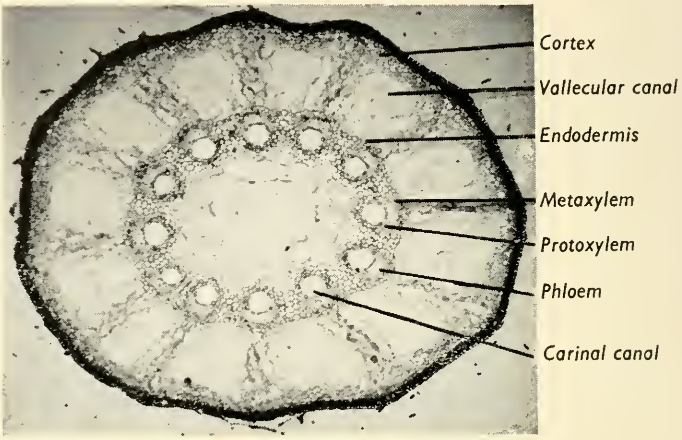

FIG. 631.—*Equisetum arvense.* Transverse section of the rhizome. Note the highly sclerotic outer cortex.

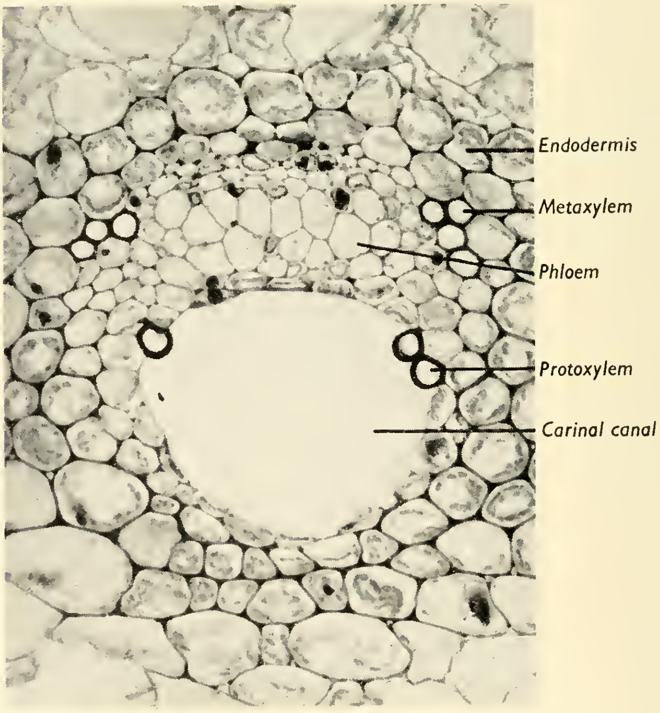

FIG. 632.—*Equisetum arvense.* A single vascular strand. Much enlarged.

bundle in the stem supplies a leaf. In *Equisetum*, however, only the protoxylem passes into the leaves, the metaxylem is entirely **cauline,** which means that it belongs to the stem alone and has no connection with the leaves.

There has evidently been considerable reduction in the evolution of this type of bundle, which is to be expected if *Equisetum* is descended from the tree-like *Calamites*. This is borne out by the expansion of the metaxylems at the nodes into a solid mass which unites with the protoxylems and obliterates the carinal canals, thus forming a continuous siphonostele. The tracheids of these nodal steles are very short and fat and are more for the storage than for the passage of water. Physiologically this water storage tissue is associated with the development at each node of a whorl of branches which obtain their supplies from it. Sections at these levels, however, are quite suggestive of the ordinary structure of the Calamite stem, for the xylem masses form a continuous woody ring.

Branch traces, which alternate with the leaf traces, are joined immediately to the nodal metaxylem. The two metaxylem strands of each internodal bundle spring directly from the nodal xylem, but the protoxylems are supplied by branches which arise from the protoxylems of the internode below. Two branches come from each protoxylem strand and, diverging to right and left, pass across the inner side of the nodal xylem, and join with the corresponding branches from the neighbouring bundles to form the protoxylem of the bundles above. This rather complicated structure may be understood by reference to Fig. 633.

The whole structure is best interpreted as a widely perforated solenostele, in which the perforations, separating the " vascular bundles," run the whole length of each internode. They have been looked upon as branch-gaps, but they show no constant relationship to the development of branches. It is not improbable that it has been developed from an ancestral form with a solid central xylem or protostele.

The solenostelic interpretation is supported by the occurrence, at the nodes only, of a second endodermis internal to the ring of vascular bundles.

From the above description of the stem we may note especially the following outstanding points ; the large intercellular spaces which are associated with the assimilatory tissue of the stem ; the small development of the xylem and phloem, which becomes particularly marked in the marsh and aquatic species of the genus, and the strong development of sclerenchyma at the outside of the stem, which replaces the xylem as a means of mechanical support.

The apex of the stem is conical, with a large pyramidal apical cell with three sides, the divisions of which follow in very regular order. The youngest internodes are very short so that the sheaths of leaves overtop the apex like a bud. The maturing internodes, however, expand so rapidly that the soft tissues are torn apart, thus forming the three series of intercellular cavities.

Branches are only formed on the green stems, not on the fertile ones. The anatomical structure of the lateral branches differs only quantitatively, not qualitatively, from that of the main axis. The number of leaves at each

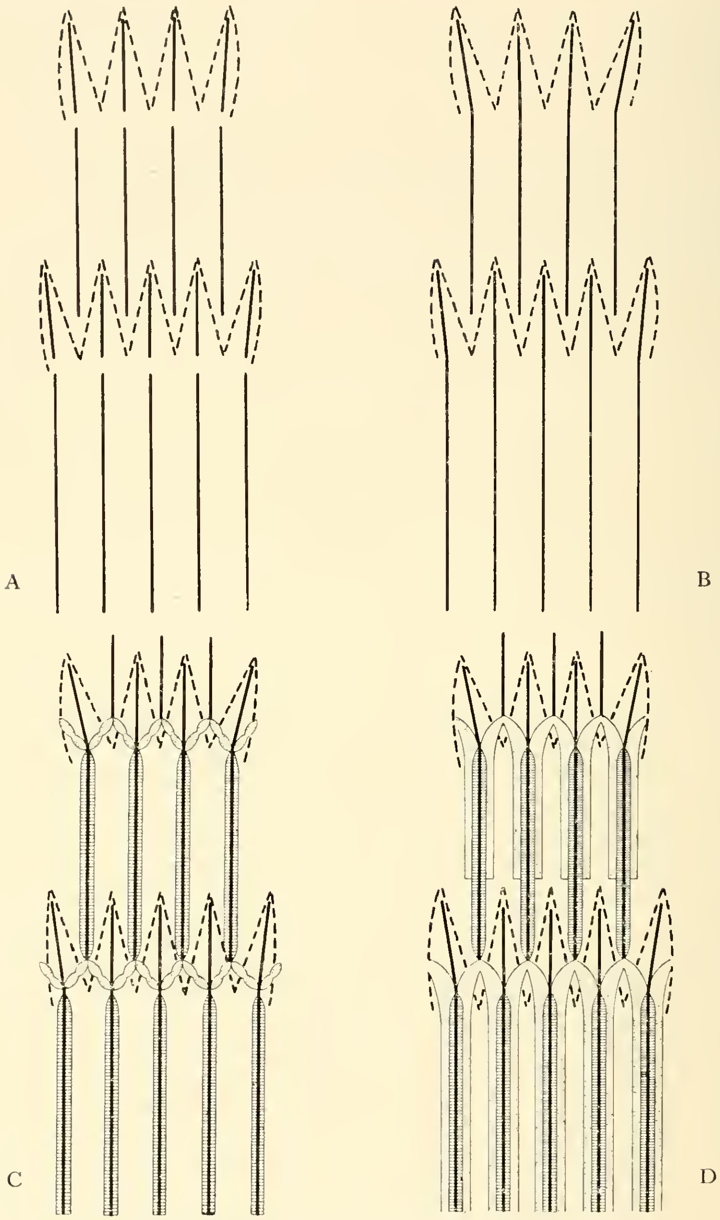

FIG. 633.—*Equisetum arvense.* Vascular structure of the stem. A, Early stage near the apex, internodal protoxylem strands and leaf trace strands still independent. Outline of leaves shown by dotted lines. B, Internodal protoxylem strands and leaf traces united, but internodal strands still independent of those in the internode above. C, Development of metaxylem at the nodes connecting the internodal protoxylem strands, which are now surrounded by carinal canals which are transversely shaded ; metaxylem dotted. D, Basipetal extension of the metaxylem in the internodes. Branch traces have been omitted. The nodal branches of the protoxylem strands lie behind the nodal metaxylem and do not appear in the figure.

node is reduced to three or four, with a corresponding reduction in the number of bundles in the stele, and the assimilating tissue is increased, forming three or four ridges along the internodes. The close relationship between the main axis and the side axes is shown by the fact that in the early stages of its development the main axis has a structure which is exactly like that of the laterals which are formed later. Furthermore, in some examples, the apex of the main stem is again reduced to this simple structure and forms a delicate prolongation above the level of the highest laterals.

The xylem system of *Equisetum* seems so inadequate for the maintenance of the vigorous water flow which can be demonstrated experimentally, that the suggestion has been made that water travels in the intercellular canals. In spring it is not unusual to find all these canals full of water under pressure, so that the suggestion of their conducting function, at least under some conditions, is probably correct.

Anatomy of the Leaf

The leaves play an unimportant part in the life of *Equisetum*, for they cannot function efficiently as organs of assimilation and probably serve chiefly to protect the lateral buds.

The tips of the leaves are free, though their lower parts are fused laterally to form the leaf sheath round the base of the internode. Each leaf contains a single vascular bundle.

The vascular bundles of the leaf sheath are simple and collateral in structure and do not possess carinal canals. Each bundle is surrounded by an endodermis. The outer tissues of the leaf sheath consist of narrow bands of sclerenchyma, which pass up the leaf ridges, alternating with the strips of assimilatory tissue associated with stomata. We thus have, on the sheath,

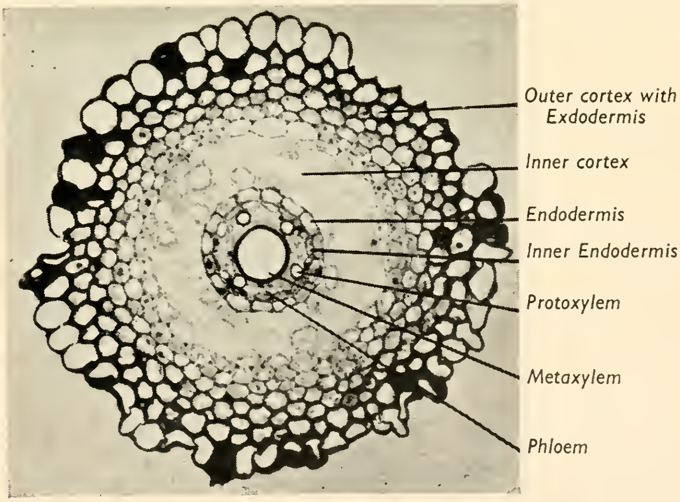

Fig. 634.—*Equisetum arvense.* Transverse section of the root.

vertical bands of stomata corresponding in number to the number of the vascular bundles. It is doubtful, however, to what extent carbon assimilation is effected by these assimilatory zones, for the plant depends chiefly on the green tissue in the stems.

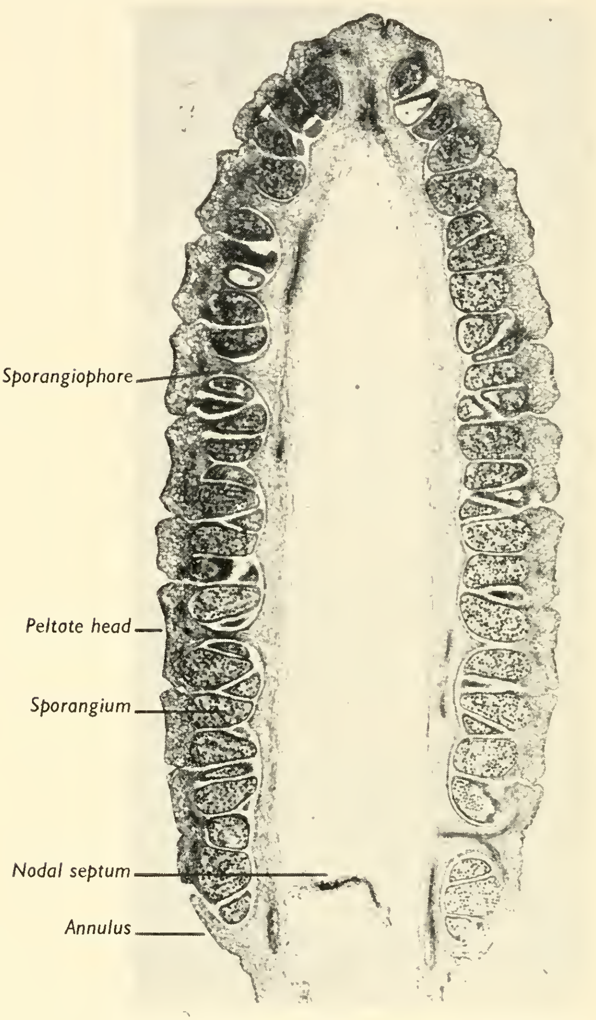

FIG. 635.—*Equisetum arvense.* Longitudinal section of the strobilus showing whorled sporangiophores with attached sporangia. The centre of the axis is fistulose and hollow except for a septum at the basal node.

ANATOMY OF THE ROOT

The roots are produced from the lateral buds, each developing one root at its base. In the rhizome they develop whether the bud grows or not, but in the stem they are normally dormant. Each root has a wide cortex, with an outer **exodermis** (Fig. 634). Inside there is a well-defined endodermis, and a small stele consisting of either three or four protoxylem groups, with phloem alternating with them, and a single, central metaxylem vessel. The chief interest in the root of *Equisetum* is the fact that the endodermis consists of two layers, a large-celled outer layer, and a smaller-celled inner layer which replaces the pericycle and from which lateral roots originate. There is a three-sided apical cell, which produces a **root cap** as well as the root tissues.

There is no main root in the mature plant of *Equisetum*, for this structure, which appears in the embryo, only lasts for a short time and is soon superseded by adventitious roots.

Development of the Strobilus

The cone of *Equisetum* is a terminal structure, arising either on the main fertile shoot or, rarely, on a branch. It possesses a fairly stout axis, giving rise to crowded, alternating whorls of T-shaped **peltate scales,** termed **sporangiophores,** on which the sporangia are developed (Fig. 635). Each sporangiophore has a short cylindrical stalk and expands at its distal end into a flat plate, on the under-surface of which from five to ten sporangia are attached (Fig. 636). The peltate heads of the sporangiophores arise in such close contact that, as a result of mutual pressure, they become hexagonal in outline. The sporangia develop towards the axis and fill up all the space that is left between the peltate scales. At the base of the cone there is a ring-like outgrowth, the **annulus,** which is sometimes toothed and which appears to be a reduced leaf sheath.

The cone axis is hollow, and although the sporangiophores are in whorls the vascular anatomy is irregular and shows no nodes or internodes. Gaps in the stele are present, but they are not directly related to the sporangiophore traces. The metaxylem is much more developed than in the stem, forming a discontinuous ring, and is in close contact with the protoxylems. The latter form the traces to the sporangiophores, passing up the stalk of the scale and dividing radially at the top, one branch going to each sporangium.

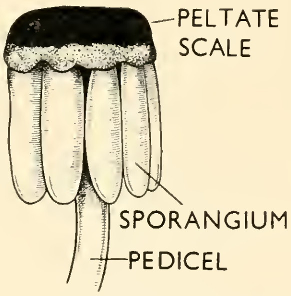

Fig. 636.—*Equisetum arvense.* A single sporangiophore showing the peltate head with ring of attached sporangia.

Development of the Sporangium

Each sporangium arises from a single superficial cell on the under side of the expanded peltate scale. This cell divides periclinally, and the inner segment gives rise to the **archesporium.** The outer segment forms part of the wall, the rest being formed from the sporangiophore. This wall is at first several cells thick, but the inner layers, termed the **tapetum,** eventually break down and form a nourishing liquid for the developing archesporium. The sporangium when mature possesses a single-layered wall composed of spirally thickened cells. It dehisces by a longitudinal split.

As the archesporial tissue develops, about one-third of its cells break down to yield their food supply to the cells near them. The surviving cells are the **spore mother cells,** each of which finally divides into four cells, during which reduction division takes place, each four cells being arranged in a tetrahedron. These are the **spores.**

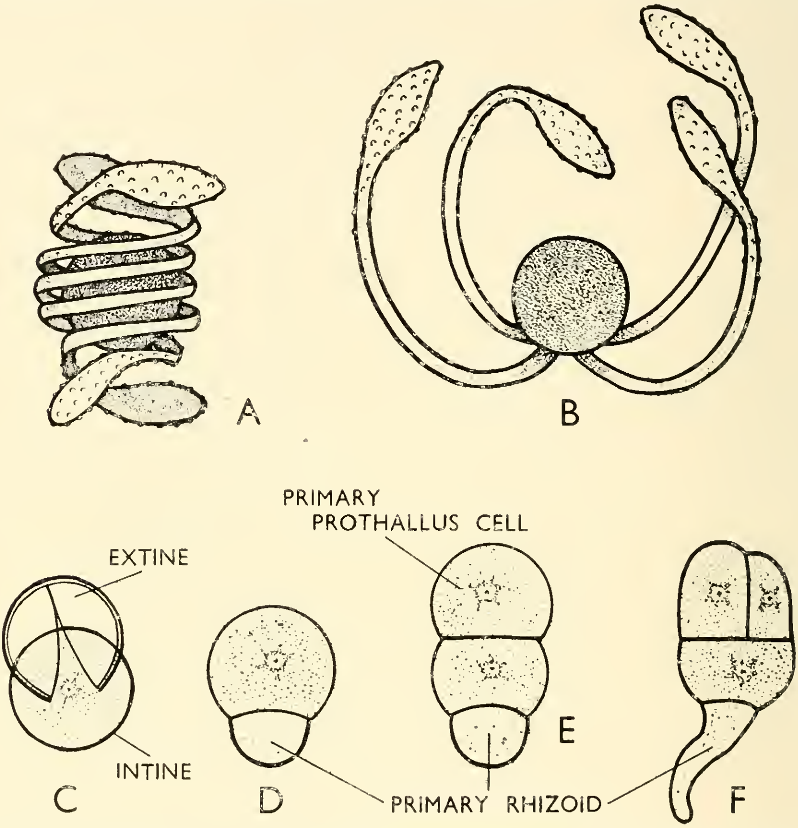

Fig. 637.—*Equisetum arvense.* Spores and germination. A, Spore showing uncoiling of epispore. B, Spore in dry air showing the four arms of the epispore uncoiled. C to F, Stages in the germination of the spore. (*Modified from Sadebeck.*)

The young spore when first formed has a thin cellulose wall, but as development continues it becomes more complicated. The membrane of the mature spore consists of four layers. The outermost layer or **epispore** splits along spiral lines into two long bands with flattened ends, called **elaters,** which, until the spore is mature, remain closely wrapped around it. When the spores are dried the two elaters stretch themselves out, crosswise, remaining attached only by their central region, and forming four distinct appendages (Fig. 637). These structures are hygroscopic, as they are cuticularized on the outer surface only, and they twist and turn according to the amount of moisture in the air. In moist air they curl up, but when they are dry they stretch out again. There is some doubt as to whether these structures assist in the dispersal of the spores, but it seems certain that they materially aid in effecting the dehiscence of the sporangium. The spores contain a number of chloroplasts, and as is usual in similar cases only remain viable for a few days.

The spores of *E. arvense* are apparently all alike, as in *Lycopodium*, and the species is said therefore to be **homosporous.** Careful observation, however, shows that there are two kinds present. If a large number are measured and their diameters plotted on squared paper it will be found that two curves are produced, with well-separated maxima and very little overlap (Fig. 638). The smaller series are much paler green than the larger ones and can be picked out by eye in a fresh sporangium. The two kinds are not equal in numbers nor is the number of each type constant in a tetrad. This is not a perfect heterospory, because though the small spores produce small male prothalli, the large spores produce hermaphrodite prothalli, *i.e.*, with both male and female organs. The case is interesting, however, as showing apparently an early stage in the development of heterospory. Some other species of *Equisetum*, especially those with sporangia on the green vegetative stems, show no difference of size among their spores. Some of the fossil Calamites, on the other hand, which were homosporous (*C. binneyana*), do show a corresponding difference of size, while other Calamite species had definitely developed true heterospory (*C. casheana*).

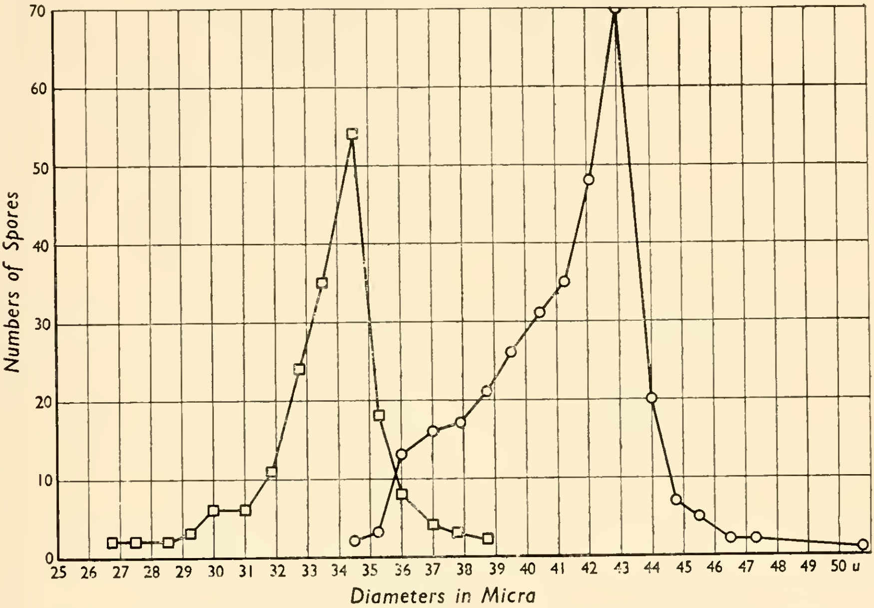

FIG. 638.—*Equisetum arvense.* Variation of spore size. The smaller and larger spores have an almost independent range in variation of diameter, the curves having widely separated modes.

THE PROTHALLUS

The spores germinate immediately on reaching the ground, and divide to form two cells of very unequal size. From the smaller cell there grows out the first rhizoid, whilst the larger cell produces the prothallus. This prothallus usually forms a flat plate of green tissue from which many filamentous branches are given out (Fig. 639). The tissue is mostly one cell thick and there is no apical growth.

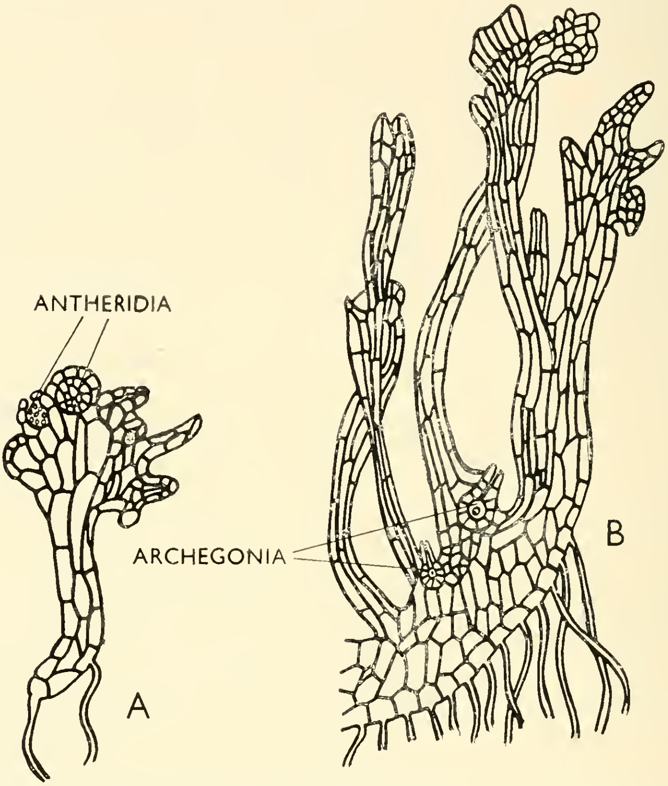

FIG. 639.—*Equisetum arvense.* Two prothalli. A, Young stage with antheridia. B, Old stage with vegetative lobes and archegonia. (*After Sachs.*)

The prothalli are of two kinds, small male prothalli which only produce antheridia, and large prothalli which are hermaphrodite and give rise to archegonia and antheridia. The large prothallus is much more branched than the small male and gives rise to a series of lobes on the lower side, between which the archegonia are produced. In both types of prothalli, as growth continues, numerous rhizoids are produced from the lower surface.

DEVELOPMENT OF THE ANTHERIDIUM

The antheridium is a very simple structure (Fig. 640). It arises from a superficial cell of the prothallus, which divides into two by a wall parallel to the external surface. The upper cell divides two or three times to form a series of **jacket cells,** one of which forms a three-sided **operculum,** whilst

FIG. 640.—*Equisetum arvense.* Prothallus with antheridia containing antherozoids.

the lower cell, after numerous divisions, forms the **antherozoid mother cells.** From each of these cells a single **antherozoid** is formed. This antherozoid

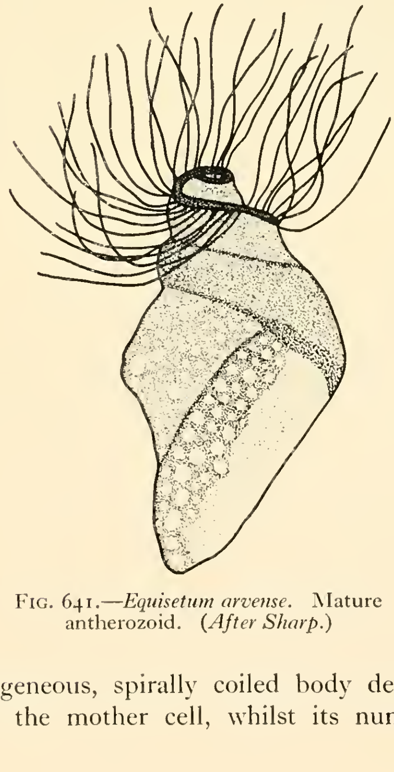

FIG. 641.—*Equisetum arvense.* Mature antherozoid. (*After Sharp.*)

consists of an homogeneous, spirally coiled body derived almost entirely from the nucleus of the mother cell, whilst its numerous apical flagella originate from the cytoplasm of the mother cell. They are attached to a narrow band, the **blepharoplast,** which lies against the anterior end of the antherozoid (Fig. 641). The antherozoid is very similar to that of the Ferns in structure and appearance, and is especially like that of *Osmunda.*

Development of the Archegonium

The archegonia arise on a cushion-like part of the large prothallus, and as fresh lobes are formed additional archegonia may be formed at their bases. At first the archegonia point downwards, as they do in the Fern, but by subsequent development of fresh lobes they become turned upwards (Fig. 642). The development of the archegonium is similar to that in the Fern, though usually no basal cell is formed. The mother cell of the archegonium divides into a **central cell** and a **neck cell.** From the central cell two **neck-canal cells** are cut off above and a **ventral cell** below, whilst the neck cell divides into three or four rows each consisting of four cells. The uppermost neck cells are long and bend back, leaving a wide opening for the entrance of the antherozoid. Lastly, the ventral cell divides obliquely to give the **ventral canal cell** and the **oosphere.**

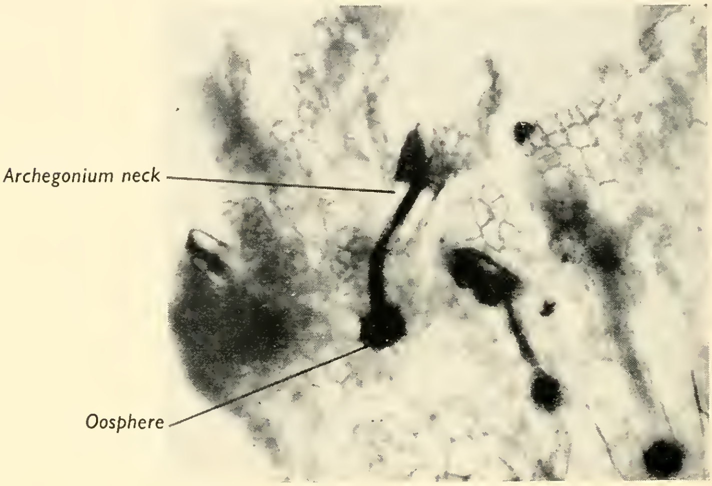

Fig. 642.—*Equisetum arvense.* Prothallus with archegonia.

Development of the Embryo

Fertilization is effected in the same way as in the Ferns by the migration of the antherozoid down the neck of the archegonium, followed by the fusion of the two gamete nuclei to form an oospore. Several archegonia on one prothallus may be fertilized and develop simultaneously.

The oospore divides into two by a horizontal wall, after which the upper cell divides, forming the initial cells of the first leaf and of the young stem.

The stem segment then cuts off two more cells which give rise to the second and third leaves, thus forming the first nodal whorl of the young plant. Meanwhile the lower cell has divided up to give rise to the main root and the foot, the latter being a comparatively unimportant structure in *Equisetum*. Very early in development the apical cells of the stem and primary root are organized (Fig. 646).

Growth now continues rapidly and the root bursts through the tissues of the prothallus, whilst the young stem grows out through the neck of the archegonium, which forms the **calyptra,** and the young plant becomes independent, though for a time it retains connection with the prothallus through the foot. In course of development the stem becomes organized in the form of the mature plant, whilst the root gradually disappears, and, as we have seen, its function is taken over by adventitious roots which arise from the underground part of the developing stem.

The primary stem grows upright until it has formed about a dozen nodes, each of which bears three leaf-teeth. It is then replaced by a more vigorous branch arising near the base of the first stem, and this in its turn by another in succession. The third or fourth of this series of branches turns downwards into the earth and becomes the rhizome of the mature plant. Anatomically the primary stem is peculiar in being solid, without the carinal canals which are present in the adult stem, and the xylem is better developed than in later shoots. At the base of the seedling there is a protostele, but the axis becomes siphonostelic at the level of the first branch.

ALTERNATION OF GENERATIONS

We see in the life-history of *Equisetum* the same alternation of generations we have met with in the other examples of the Pteridophyta. There are, however, certain interesting points which arise in this example. Unlike

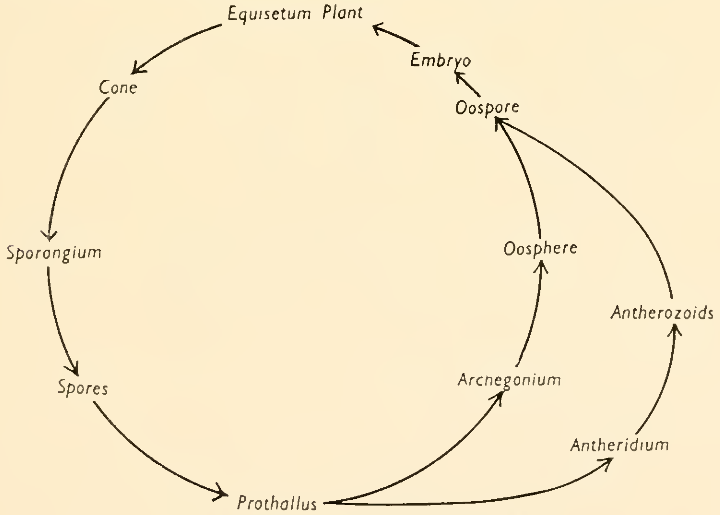

FIG. 643.—Life-cycle of *Equisetum arvense*.

the Fern, two types of prothalli are formed, one bearing the male, and one bearing male and female sex organs, but both types are free-living and are not attached to their respective spores, as in the case of *Selaginella*. In

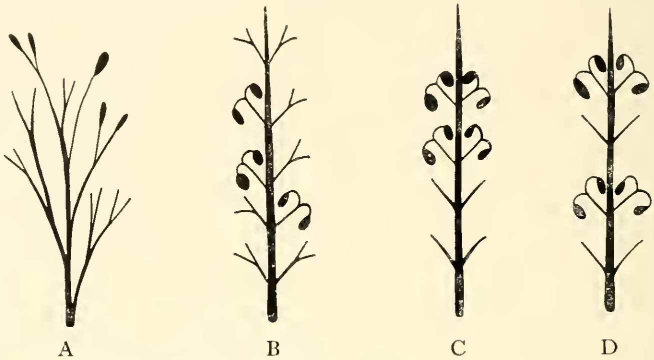

FIG. 644.—Development of the strobiloid condition from the Psilophytalean condition. A, *Psilophyton* with separate dichotomous sterile and fertile telomes. B, *Asterocalamites*. Sterile and fertile telomes in mixed whorls. C, *Equisetum*. Fertile telomes grouped in whorls to form a terminal strobilus. D, *Calamites*. Sterile and fertile whorls of telomes alternating. (*After Zimmermann.*)

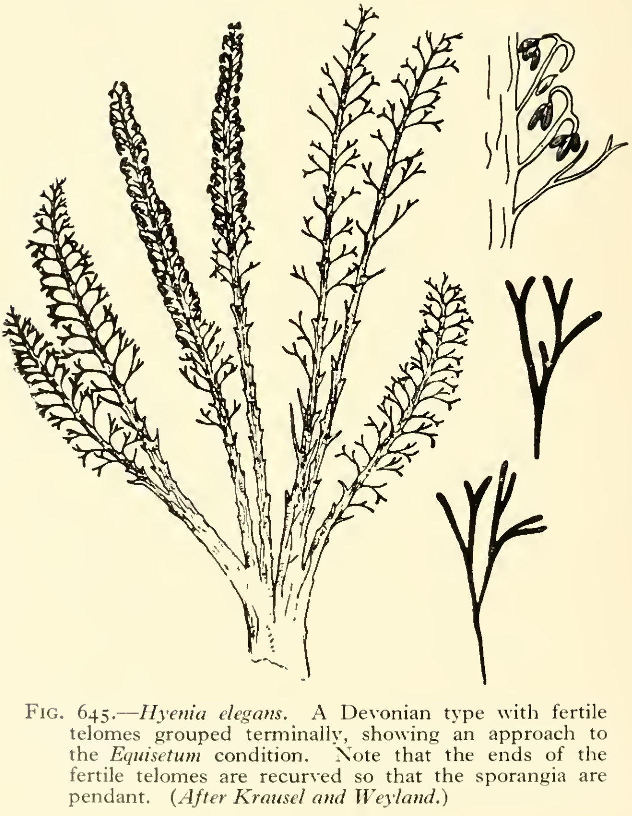

FIG. 645.—*Hyenia elegans*. A Devonian type with fertile telomes grouped terminally, showing an approach to the *Equisetum* condition. Note that the ends of the fertile telomes are recurved so that the sporangia are pendant. (*After Krausel and Weyland.*)

Equisetum the spores are all alike, although recent investigations have shown that there is a slight variation in the size of the spores, suggesting that possibly we have here the beginning of a heterosporous condition. *Equisetum*, therefore, may be said to occupy an intermediate position between the Fern with a purely homosporous sporangium giving rise to only one type of free-living prothallus, and *Selaginella* with its typical heterosporous condition and unisexual prothalli.

The life-history of *Equisetum* can therefore be illustrated by Fig. 643.

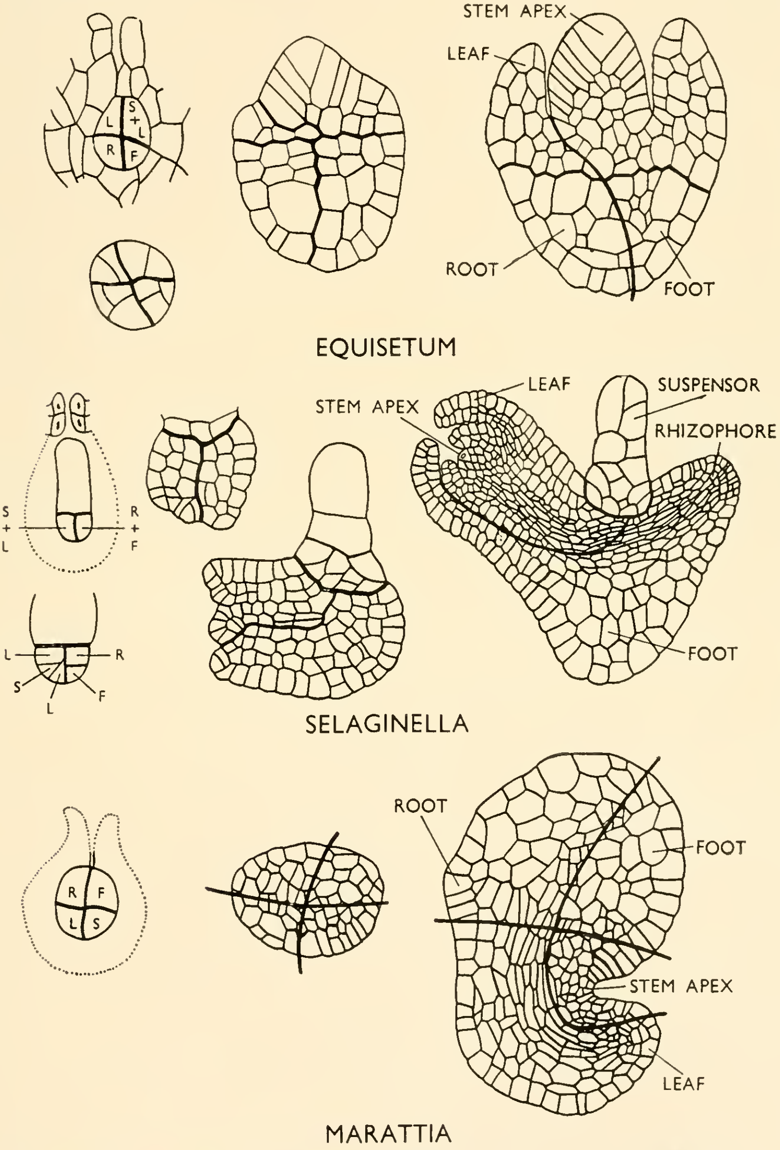

Fig. 646.—Comparative embryology of *Equisetum*, *Selaginella* and *Marattia*. F = foot; L = leaf; R = root; S = stem apex.

RELATIONSHIPS OF EQUISETUM

The relationship of *Equisetum* to *Calamites* and *Sphenophyllum* has been mentioned above. Both these ancient types, however, had cones with leafy sporophylls, and the question has been much debated whether the leafless cone of *Equisetum* is a primitive condition or not. Anatomically there is no trace of any sporophylls having formerly existed, and the opinion has gained ground that we have in this genus a point of contact with a very ancient form of organization.

Briefly this view, as put forward by Zimmermann, is based upon the existence in the most primitive plants of primary branches of a very simple type, which he calls **telomes.** Some of these bore terminal sporangia and were thus fertile, others were sterile, but both were morphologically equivalent. This structure is actually represented by the Devonian fossil *Psilophyton* (see Fig. 644). From this may be derived a condition, shown by *Asterocalamites*, in which the two types of telome were in whorls, mixed together. By another line of development we get the Devonian fossil *Hyenia* (Fig. 645), in which the fertile telomes were collected together on the upper parts of certain branches, and the sterile telomes on the lower parts. From this condition Zimmermann suggests that *Equisetum* has been evolved, while in the Calamites fertile and sterile whorls alternated on the upper parts of the stems which became finally differentiated as cones.

It has been customary to refer to the cone appendages in *Equisetum* as **sporangiophores,** but this is purely a descriptive term, while the use of the term telome connects them definitely with those primitive thallus lobes from which both branches and leaves may have been divergently evolved.

CHAPTER XVI

THE SPERMATOPHYTA: GENERAL INTRODUCTION WITH AN OUTLINE OF EVOLUTIONARY MORPHOLOGY

The Spermatophyta,[1] commonly called the "Seed Plants," is the large group of plants in which the chief organ of distribution is the **seed.** By this term is implied a structure enclosing an **embryo** and protected by a special covering, the **testa.** A store of reserve food material is also present, either in the tissues of the embryo itself or in a special tissue, the **endosperm,** which surrounds the embryo.

The Spermatophyta have no doubt evolved from some lower group among the Cryptogams, most probably from among the Pteropsida, but their evolution took place at an early geological period, and their direct ancestors have long been extinct. This evolutionary process depends essentially upon the reduction of the gametophyte generation and its enclosure within the tissues of the sporophyte, which thus became the only externally visible generation in the life-cycle. We shall see later how this took place and what were its biological consequences. It is noteworthy here, however, that the tendency to a reduction of the gametophyte can be seen even among Ferns with free-living prothalli, in which the precocious development of sex organs on small prothalli is not uncommon. Goebel even records a case of a Fern prothallus consisting only of one vegetative cell, which had produced two antheridia.

The reduction and enclosure of the gametophyte has only been rendered biologically successful by the development of another new device, peculiar to the seed plants, namely the transport of the male gametic cells to the immediate neighbourhood of the female, in place of the free-swimming antherozoid. This has involved two stages. The first is **pollination,** that is, the provision of means whereby the microspores are conveyed to the immediate neighbourhood of the megaspore and are there held while they germinate. The second is the evolution of the **pollen tube,** as an outgrowth from the microspore, which ensures the direct access of the male cells to the female, without exposing them to the hazards of an external journey. The importance of the latter factor can scarcely be overrated. It is the ultimate answer to the problems of fertilization under land-living conditions and serves to separate two great biological groups, the **Zoidogamia,** which include all plants with free-swimming antherozoids, and the **Siphonogamia,**

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[1] The term Spermatophyta is now generally used in preference to the older term Phanerogam, which is based on a false antithesis to Cryptogam. The term Spermaphyta is sometimes used but is not etymologically correct.

which include all those with pollen tubes. These are not regular systematic classes, because the division cuts across the Gymnospermae, among which there are some primitive types which still retain antherozoids, although they are pollinated like the higher types.

CLASSIFICATION

There are three main sub-phyla included in the Spermatophyta :—

Pteridospermae (Seed-bearing Ferns) (Extinct). Plants with Fern-like leaves on which were borne microsporangia and megasporangia, the latter producing seeds. The sporophylls are not usually distinguishable from the foliage leaves and are not aggregated together to form a flower (see Volume III).

Gymnospermae (Naked-seeded Plants) (Living). Plants, mostly trees, in which the sporophylls have been reduced, so that they no longer resemble the foliage leaves, and have been aggregated into strobili or cones, which constitute **flowers.** The microsporangia and megasporangia are separated usually into different strobili. The seeds are not enclosed.

Angiospermae (True Flowering Plants) (Living). Plants which include trees, shrubs and herbs. The sporophylls are aggregated into **flowers** which may be hermaphrodite, with both microsporangia and megasporangia or unisexual with one type of sporangium only. The megasporangia are enclosed in **ovaries,** which, after the fertilization of the oosphere, ripen into **fruits** (Fig. 647) (see Volume II).

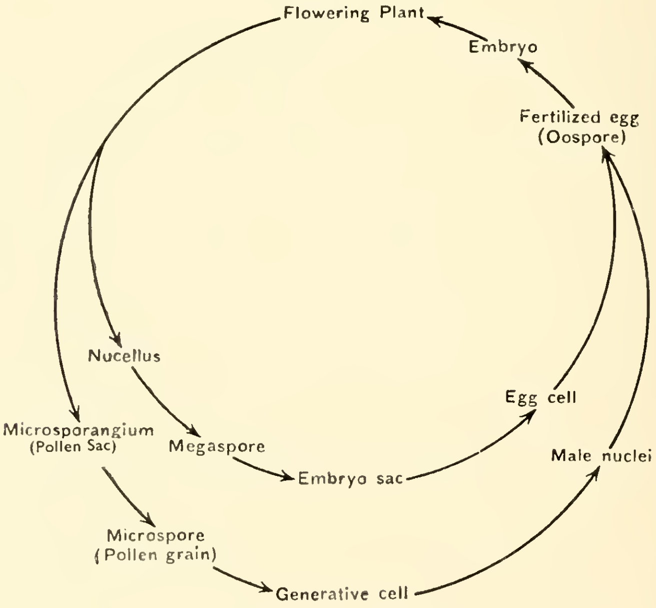

FIG. 647.—Life-cycle of the Spermatophyta.

The Evolution of the Seed

In the previous groups of plants which we have considered, the principal organ of dispersal is the spore, the germination of which produces a gametophyte.

In the lower types this gametophyte is often an independent plant, which in many cases, especially among the Algae, is structurally similar to the sporophyte. An evolutionary process of reduction is, however, traceable in the history of the gametophyte, a reduction both in size and in independence, so that in *Selaginella* we see a stage at which the gametophytes, which have become unisexual, remain enclosed within the walls of the spores which produce them. The female gametophyte, inside the megaspore, is, however, much bigger than the male and is provided with a store of reserve food material. The growth of the embryo from such a gametophyte is largely external to the prothallus, and its establishment as an independent plant takes place directly and without any intervening period of rest.

The essential change which led from this condition to that of the Spermatophyta was the retention of the megaspore within the megasporangium and its fertilization *in situ*. One or two species of *Selaginella*, notably *S. apoda*, show this actual change (Fig. 648). Only one megaspore is formed in each megasporangium and it germinates without being shed. The young embryos develop in the shelter of the sporangial wall and of the sporophylls, and are only dropped when they are already provided with a root and a primary shoot.

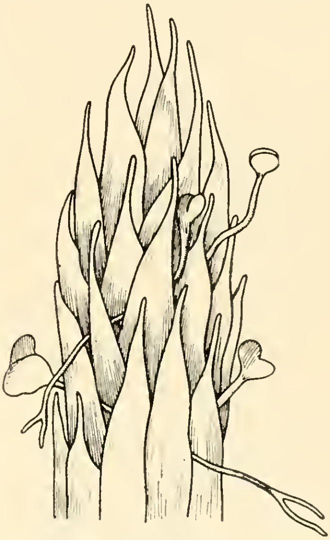

FIG. 648. — *Selaginella apoda*, showing sporelings from megaspores which are still *in situ* on the strobilus. (*After Lyon.*)

While this illustrates clearly an intermediate stage in the evolution of the seed it does not make *S. apoda* a true seed plant, because a further step is required by which the female prothallus, the megaspore and the megasporangium eventually become integrated into a new compound structure, the **seed,** which functions as a biological unit and is detached from the plant and dispersed as a unitary structure.

The equivalence of the female reproductive structures between the Spermatophyta and the Pteridophyta may be summed up in the following terms.

In the Pteridophyta we have four separate entities; the female prothallus, the megaspore, the megasporangium and the megasporophyll.

In the Spermatophyta the female prothallus is permanently retained in the megaspore, the two together constituting the **embryo sac.** The megaspore is likewise permanently retained in the megasporangium, which becomes thick-walled and fleshy, and is known as the **nucellus.** The nucellus in its turn has been enclosed within one or two coverings called the **integuments,** which are of uncertain morphological nature, but are probably related to the cupules that surround certain Pteridosperm seeds. All the above elements together constitute the **ovule.** Among the Gymnosperms the ovules are attached directly, without any further protection, to the female sporophylls. In the Angiosperms the ovules in their turn are enclosed in a case, the **ovary,** which forms a part of the organ called the **carpel,** a structure of great importance because it forms the **fruit,** which is the distinguishing mark of this, the highest group of the Seed Plants. The carpel probably represents a development of the megasporophyll (Fig. 649). We shall return to a further discussion of seed structure and behaviour in Volume II.

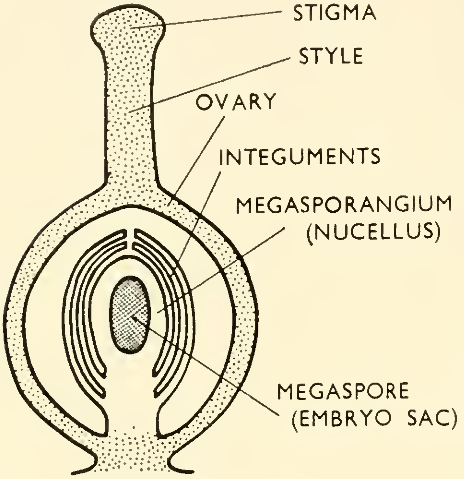

Fig. 649.—Diagrammatic section through an angiospermic carpel with enclosed ovule, showing the various parts.

Although the megaspore and the megasporangium have thus undergone a marked change in relationship and also in structure during the evolution of the seed, the microspore and the microsporangium have remained relatively unaltered and are recognizable in the Flowering Plants as the **pollen grain** and the **pollen sac** respectively.

The evolutionary process seems to have taken place at a very early geological date and in more than one group of plants. Some members of the Lycopodiales seem to have arrived at the seed habit quite independently, notably the genus *Lepidodendron*, but they did not succeed in evolving into Flowering Plants, possibly owing to some deficiency in their anatomical structure.

On the other hand, we find in the Carboniferous rocks a group of plants showing close similarities with the Ferns, which bore seeds upon their fronds. The name Pteridospermae, given to this group, indicates their intermediate position. They are the most primitive seed plants in the Pteropsida and they never themselves produced the special aggregation of sporophylls which we call a flower, though they probably represent the stock from which the Flowering Plants have been derived, as the latter are certainly Pteropsid rather than Lycopsid in their affinities.

Biologically the evolution of the seed was an immense gain. Within its protective covering the embryonic plant develops in safety ; by mechanical developments of this same covering it is successfully dispersed and by the stores of reserve food which the seed contains it is tided over the critical and dangerous period of its establishment as an independent plant. When we contrast these advantages with the relatively imperfect provision made for the safety and establishment of the young plant in lower groups we can easily understand why the Seed Plants have become dominant in the world's vegetation.

Seed production in the Angiosperms is more efficient than in the majority of Gymnosperms, in that fertilization in the higher group occurs at an earlier stage of seed formation than in the lower group. In many Gymnosperms the seed is completely developed and may in fact be actually shed from the tree before fertilization, and should any accident prevent its accomplishment the whole of the material involved is wasted. The angiospermic ovule, however, is fertilized while still quite young, and unless it takes place there is no further development. Thus the laying down of reserve food in the endosperm, for example, is a post-fertilization process, in contrast to the prothallus formation of the Gymnosperm which precedes fertilization.

The whole of this development hinges on one cardinal fact: the reduction of the free-living gametophyte, which, as the seat of sexual conjugation, is inseparably linked to watery conditions, and its enclosure within the body of the sturdy sporophyte, which has no such limitations. With the gametophyte thus enclosed, sexual conjugation takes place in an internal environment, free from exterior influences, and the growth of the embryo from the fertilized oosphere is likewise protected and ensured.

Evolution of the Megaphyllous Strobilus

We have seen that the Pteridosperms had no flowers. Their seeds were borne, exposed and usually singly, on the fronds. In some types these fertile fronds were leafy and were otherwise indistinguishable from the sterile fronds, just as in *Dryopteris* at the present day, but in others the fertile fronds had no lamina and were reduced to simple or branched stalks, which bore either microsporangia or seeds, the latter sometimes protected by a cup-like cupule. It is immaterial for our present purposes to discuss whether these specialized fronds or sporophylls were in fact evolved from leaves like the foliage leaves, or whether the two had always been distinct structures. Either view may be correct, but the important thing for us to notice is that in certain types the production of sporophylls became restricted both in time and space, so that they formed limited groups, either on the main axis or on side shoots, where they were arranged in the same spiral succession as the foliage leaves but closely aggregated to form strobili. This re-emergence of the strobilus, a structure otherwise limited to the microphyllous Lycopodiales and Equisetales, as an aggregation of megaphyllous seed-bearing sporophylls, marks the beginning of the true Flowering Plants.

It seems to have occurred first, so far as the megaphyllous Pteropsida are concerned, in the Palaeozoic Cordaitales (Figs. 650 and 651). What relation these plants bore to the Pteridosperms is uncertain, but it is probable that both groups were descended from a common fern-like ancestry, the Cordaitales having evolved the strobilus and the Pteridosperms alone having maintained the primitive non-strobilate arrangement of the reproductive structures which characterizes the Ferns. The close proximity of female gametophytes in a strobilus obviously increased the chances of fertilization for each of them, and this type of arrangement offered possibilities of evolution into the flowers of to-day, while the handicap of their less efficient organization brought the Pteridosperms to early extinction.

The Cordaitales themselves probably did not give rise to the modern Flowering Plants, though they may have survived into Mesozoic times. The ancestral fern-like complex, however, evolved along several different lines and another strobiloid offshoot, the Cycadales, has survived to the present day, and appears to be at least related to the forerunners of the Angiosperms.

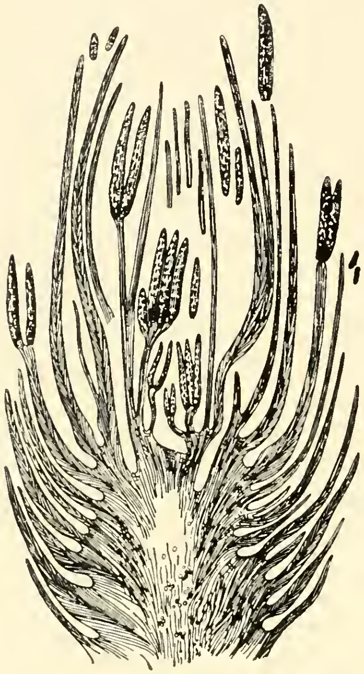

Fig. 650. — *Cordaites penjoni.* Longitudinal section of a microsporangiate cone. (*After Renault.*)

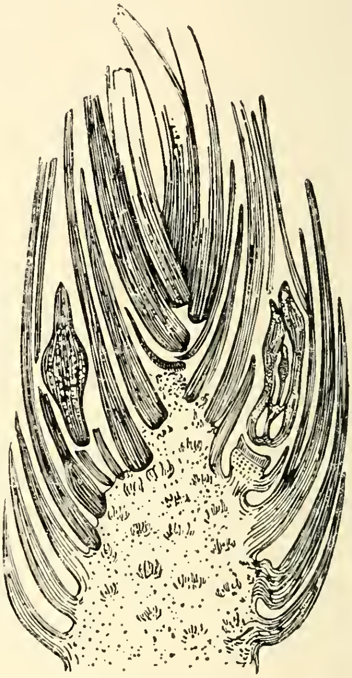

Fig. 651.—*Cordaites williamsoni.* Longitudinal section of a megasporangiate cone with seeds. (*After Renault.*)

The lowest group of the Flowering Plants is therefore that in which seeds are borne uncovered on sporophylls arranged in a strobilus or cone, and this group is called the **Gymnospermae** or naked-seeded plants.

We will only note in passing that they are almost all trees, and that the development of secondary xylem, of which we have seen only traces in the lower groups, has, with the adoption of the seed-habit, been increased to an enormous extent, so that these plants build up in the course of years large woody trunks like those of the Pine and the Yew.

This tree growth shows the descendants of the Pteropsida again doing something which the Lycopsida had already done at a lower evolutionary level in the Lepidodendrons. The parallelism in the two groups is very interesting and raises the question of a connection between strobilus formation on the one hand and tree growth on the other. Present evidence is, however, against the assumption of an evolutionary linkage between them. The differences of structure are in fact profound, and it would seem that we are here presented with an instance of evolutionary convergence. The two alliances, having been forced, so to speak, along the same path by fundamental factors of the environment, were obliged to solve the same problems independently by closely similar means.

Evolution of the Angiospermic Flower

Above the Gymnosperm level the next stage in evolution has been the enclosure of the seed within a covering, the **carpel,** formed possibly from the appendage which bears it. The embryo thus acquires yet another protection, one which is capable of great morphological variation and hence is very useful in the evolutionary sense. This brings us to the highest group, the **Angiospermae** or plants with seeds enclosed in a vessel (Gr. *aggeion*), which begins as a carpel and later develops into a **fruit.** So vast and multifarious is this group that a large portion of the rest of this book will be needed in which to deal with it.

The Angiosperms are the dominant form of plant life over the greater part of the world, and they include almost all the plants with which we are familiar in field, woodland or garden. They have shown unrivalled plasticity in adapting themselves to every form of environment, from deep lakes to deserts, and from the bed of the sea to high mountain peaks. The same power of variation is shown in the production of species numbering hundreds of thousands, which display almost every conceivable variety of plant form.

This immense success is due to a combination of many advantages, but we may perhaps point to three which have certainly played a great part : (1) insect pollination, (2) the development of many devices for seed dispersal and (3) the herbaceous habit.

It is a far cry from the Pine Cone to the Rose, and we may well inquire what connection can be traced between them. What agency could bring about the transformation of a hard, woody, uninviting strobilus into the soft, tinted and perfumed Queen of Flowers ? The answer is insect pollination and the preference of certain insects for just those qualities which distinguish the angiospermic flower from the cone. It is not for us that the Rose and Violet bloom, it is for the bees !

Recognizable Angiosperms first appeared at the end of the Jurassic period, and in a relatively short time afterwards we find many fossil types which are apparently similar to genera still living. It is a dramatically rapid step in evolution, which we can only understand if we suppose that there must have been some entirely new and powerful factor at work

As the changes which took place produced floral structures which we know, in the related living types, to be functionally connected with insect pollination, it is not unreasonable to consider that it may have been the adoption of this intimate connection with the insect world. The groups of insects chiefly concerned in pollination were themselves rapidly evolving at the same period, and this may have given the necessary stimulus to the evolution of the flower, by rapidly and strictly selecting all those forms in which coloured sporophylls, perfume glands or nectar glands, provided attractions for insect visitors.

The Angiospermic flower is usually bisexual or, more strictly speaking, **amphisporangiate,** with the female part placed above the male part, which is the reverse of the order typical of the Lycopod strobilus. Whether this was the original condition we cannot say. Most Gymnospermic cones are unisexual, but hermaphrodites occur as abnormalities in some families, and in such cases it is noteworthy that the seed-bearing sporophylls are uppermost in the cone. In one fossil group, the Bennettitales, the cones are, in fact, normally bisexual, with the megasporophylls above the microsporophylls, and in this, as in some other respects, they resemble Angiosperms more closely than do the other Gymnosperms.

The close association of the sex organs together in one strobilus may well have conferred a biological advantage which led to a condition which was abnormal in most Gymnosperms becoming normal in the Angiosperms.

The development of effective means of seed dispersal reaches heights of complexity in the Angiosperms which far exceed anything in other groups, even in the Gymnosperms. The importance of this in contributing to their world-wide distribution needs no emphasis, but apart from its geographical aspects, wide dissemination has an indirect evolutionary consequence, through the introduction of the offspring of single plants into many different environments, which encourages the selection and perpetuation of variants which may have certain qualities adapting them to specialized conditions. There can be no doubt that the natural selection of such specialized variations has played a great part in creating a multiplicity of species.

Vegetative Habit in the Angiosperms

The herbaceous habit in Angiosperms seems to have been a secondary development from the tree habit. In those families which we can recognize by their floral characters as primitive there is a predominance of trees and shrubs, while the most advanced families are chiefly herbaceous. We shall refer later (p. 909) to the anatomical aspects of this change, but from the evolutionary standpoint its influence is manifested in the consequent shortening of the life period of the individual. Many herbs flower and form seeds within a year or less. A tree, on the other hand, may be anything up to thirty years in reaching the flowering stage, which, apart from the delay, implies greater risks of injury or death before the individual can perpetuate itself. The result of this contraction of the individual life-span is that a herbaceous species passes through many more generations in a given time than does a tree species. Every flowering period implies sexual reproduction, with its concomitant possibilities of variation, and thus there has been a marked acceleration of the tempo of evolution in these short-lived types.

The foregoing remarks all tend to emphasize the importance of the relation between the plant and its environment, that is to say, the kind of consideration which is called Ecological. Ecology, in fact, almost dominates the botanical treatment of the Angiosperms, to the subordination of the purely morphological outlook which usually prevails in the treatment of lower groups. The principal reason for this difference seems to be that the vast multiplicity of forms among the Angiosperms makes it impossible for any individual worker to study thoroughly the morphology of more than a very small proportion of them. The time has not yet come when a comprehensive morphological treatment may be possible, except perhaps in relation to some of their sexual structures, in which there is some degree of uniformity. The vegetative morphology can only be treated in the barest outlines and with reference to one or two fundamental attributes.

Morphology of the Shoot in the Spermatophyta

The old-fashioned morphologist studied form purely as an aid to classification, and he therefore classified the types of form which he observed as fixed and static things, assigning to each type of form a name and a definition. Such types represented a series of Platonic ideals or concepts to which the visible world was assumed to conform. The kinetic views of modern evolutionary biology have swept all this away into the limbo of forgotten artificialities. We now regard all forms as part of a universal evolutionary flux, and the end we pursue is, not the precise discrimination of forms from one another, but the opposite, namely, an understanding of their relationships to each other and of their transformations during the march of time.

When we apply such an idea to the study of spermatophytic structure, we can see that it is possible to get an idea of the evolutionary morphology of some at least of their structural elements, in relation to the structure of lower groups.

The Spermatophyta are " cormophytes," that is to say that they, like the Pteridophyta, have three sorts of vegetative organs, stems, leaves and roots, but to treat these as fixed categories would be a reversion to the older morphology which we have condemned. If we go back into the past and endeavour to judge by the fossil evidence and by comparisons with lower groups of living plants, we may expect to find these categories merging together and blending into some common unity, as we go lower and lower in the scale of organization. That is to say that we should not regard them as fundamentally distinct but as having had a common evolutionary origin.

Although the Spermatophytes share this cormophytic organization with the Pteridophytes, they differ from them markedly in one aspect of internal organization. The vascular system of the Ferns belongs essentially to the axis or stem. Its development is correlated with the size of the stem, and the strands which supply the leaves are only subsidiary branches from the cauline (*i.e.*, axial) system. The vascular bundles of the Spermatophytes are, on the contrary, all part of a system " common " to both stem and leaf. The cauline vascular system has disappeared and every strand in the stem is destined sooner or later to form part of the supply passing to a leaf.[1] It is even doubtful whether there is any cauline vascular tissue in the apical meristem, and it is probable that in all normal cases the earliest appearance of vascular tissue at the apex is in connection with the leaf rudiments. This is a very significant difference, which invalidates any direct comparison of the vascular structure in a Pteridophyte stem and Spermatophyte stem. The leaves, which are the principal evaporating surfaces of the plant, have thus become linked directly to the roots, which are the sources of the water supply, and the amount of vascular tissue formed is proportionate to the development of the leaves rather than to the development of the stem. In other words, the development of the stem itself is dependent on the development of the leaves, and it is no longer, as in the Pteridophytes, an independent entity, and hence the plant gains in physiological efficiency.

The Strobilar Theory

There are two main theories of the evolution of the cormophytic type of body ; but they are not mutually exclusive, for one may be said to extend the other. The older theory is called the **strobilar theory,** and it has been chiefly expounded by Bower. He defined a strobilus as a spike of fertile appendages, borne in a terminal position on the shoots. The vegetative region below is so similar in structure to the strobilus that it is to be regarded as derived from it by the abortion of the sporangia in the lower regions of the shoot. This idea is illustrated by *Lycopodium selago* (Fig. 652), in which sporangia are formed in recurrent zones on the shoot, from the base upwards, while the sterile zones between show abortive sporangia in the leaf axils.

Thus on Bower's view the most primitive condition of the vascular plant is one with an axis bearing leafy appendages which all carried sporangia, the whole plant being one continuous strobilus.

Although the most typical strobili are characteristic of the small-leaved Pteridophytes, it is claimed that the large-leaved Ferns and their allies also conform to the above theory, the spiral succession of leaves upon the main axis constituting, in effect, a large strobilus, in which sometimes all, sometimes only certain groups of the leaves are sporangiferous. Such a view obviously does not recognize any essential difference, except in size, between the Fern leaf and the Lycopod leaf.

Bower then goes further to speculate on the primitive relationship of the axis and its appendages. He points out that there are at least three possible

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[1] To avoid any possible misconception it might be well to point out that the conventional way of expressing a vascular connection as " passing " from one organ to another does not imply any actual motion, any more than when we say a road " runs " from A to B.

views of this relationship. (1) That the axis pre-existed and that the leaves originated as lateral outgrowths from it. (2) That branches and leaves both originated from the differentiation of a system whose divisions were originally all alike. (3) That the leaf was the primitive structure, in the form of a thalloid body, the basal part of which assumed the form of an axis bearing the leafy portion.

The *first view* may be called the classic scheme of plant morphology, and it is that upheld by Bower himself. He considers the leaves to have arisen by direct outgrowth from a primordial leafless axis, in a manner similar to their actual origin at the growing point of a living plant.

FIG. 652.—*Lycopodium selago.* Complete plant with sporangia in the axils of undifferentiated leaves. Half natural size.

The *second view* assumes that **dichotomy,** or division of the shoot into equal portions at each branching point, is primitive, and that the development of the condition in which there is a principal axis bearing laterals (which is normal in the higher plants) has been arrived at by a process of "overtopping." This implies the unequal growth of the two segments of a dichotomy, whereby one segment assumed a leading position and the other segment took the character of a mere appendage to the leader, becoming eventually, in many cases, dwarfed to the condition of a lateral bud, which might or might not grow out into a branch (Fig. 653). It is true that dichotomy does seem to have been the earliest type of branching, at least in vascular plants, and it is possible that this scheme may truly represent the evolution of the higher **monopodial** system of branching, but it is doubtful whether this view has anything to do with the evolution of leaves as distinct organs, except perhaps, as we shall see later, in the Ferns.

The *third view* involves an attempt to harmonize the thalloid type of organization with the radial type characteristic of vascular plants, for which there is no warrant. It is true that so far as the Bryophyta are concerned the establishment of an axis with leafy appendages from a flat dichotomous thallus may possibly have occurred, and Fig. 654 shows an example of existing forms which, by comparison, illustrate how it may have come about. There is, however, no evidence that the vascular plants had thalloid, dorsiventral ancestors, and the probabilities are against it. Among the Algae radially organized and thalloid types are both frequent and are quite independent. The difference of habit, based upon the filament and the flat plate of cells respectively, may be traced even amongst the simplest forms. There is thus no reason for excluding the possibility that the radial type of organization might be ultimately derived from the filament form, by direct descent, without passing through a thalloid phase. This third view is, in fact, an illegitimate extension to primitive conditions of the **phytonic** ideas of construction, considered later in this chapter, which are derived from the higher plants and should be applied only to them, if at all.

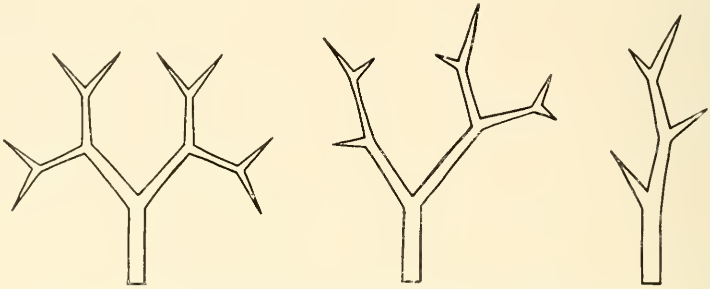

Fig. 653.—Diagram illustrating the process of " overtopping " to produce a monopodial shoot from a dichotomous shoot.

Fig. 654.—*Aneura eriocaulis.* Complete plant to show the differentiation of a thallus into an axis with leafy appendages and leafless branches at base functioning as roots. (*After Goebel.*)

Relationships of Stem and Leaf

We shall obtain a clearer insight into these problems if we consider briefly some points of structure in existing leaves and try to judge whether they are all comparable organs with a common evolutionary origin.

Jeffrey has emphasized that in the living groups Lycopodiales, Equisetales, Psilotales and probably the Isoetales, the leaves are small in relation to the axis and that they are supplied by vascular strands which cause no gap where they leave the stele. The strands which supply branches do, however, leave gaps in the stem stele, filled with parenchyma. In the Filicales and in all the Spermatophyta the leaf traces themselves make leaf gaps in the stele. The leaves in these groups are relatively large, and a physiological reason for the leaf gaps may lie in the fact that through them there is continuity between the parenchyma of the cortex and of the medulla, thus throwing open the medulla as well as the cortex for the storage of carbohydrates elaborated in the leaves. Jeffrey called the Lycopodialean type **microphyllous** and **cladosiphonic,** because only the branch traces cause stelar gaps, while he called the Filicalean type **megaphyllous** and **phyllosiphonic.**

He laid great stress on the systematic importance of the distinction, and he called the chief microphyllous alliance the **Lycopsida** and the whole megaphyllous alliance the **Pteropsida,** which includes not only the Ferns but all the Spermatophyta which share the megaphyllous character and which are assumed to be more or less directly of Filicalean descent. The Equisetales and the microphyllous fossil order **Sphenophyllales** formed the **Sphenopsida** (Articulatae) (Fig. 655), while the leafless Psilophytales and Psilotales are combined under the name **Psilopsida.** Goebel has objected to this view that the difference is merely one of relative leaf size, and he has pointed out that in some of the smallest Ferns the leaves make no stelar gaps. This is not a conclusive argument, for in *Azolla* on the other hand, which is one of the most reduced Ferns, there are leaf gaps present. It must be accepted that the difference is a very ancient one, that the two types have been separated

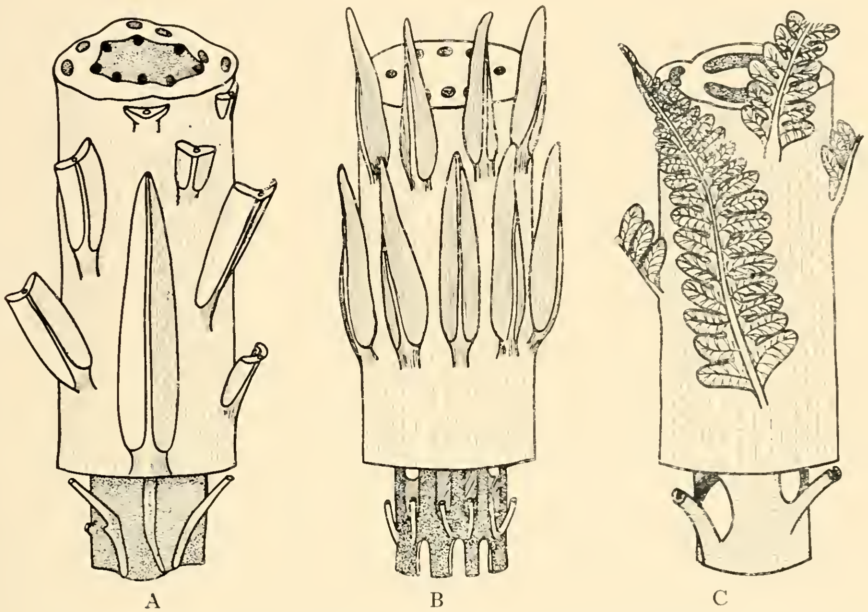

Fig. 655.—Comparison of the shoot architecture in the Lycopsida, Sphenopsida, and Pteropsida. A, *Lycopodium* type. B, *Equisetum* type. C, Fern type. (*After Jeffrey.*)

in descent from a very early stage, and that there is a reasonable doubt whether the two types of leaf are morphologically equivalent.

The Telome Theory

The second morphological theory, which was mentioned on p. 646, throws further light on the question. It is called the **Telome theory** and is due to the work of Zimmermann. He goes back to the earliest and simplest type of vascular plant known, that in the Psilophytales (see Volume III) in which the body consists of branching leafless axes, which are all substantially alike. In some cases these may be arranged dichotomously, in others monopodially, and the difference may have arisen by " overtopping," as has been suggested above, but in either case Zimmermann regards these naked axes as the primitive units of construction of the cormophyte, which is thus regarded as primarily a system of axes. Each of the terminal branches in such a system he calls a **telome.** Each telome is an ultimate branch on an older axis or **mesome.** Some telomes are sterile, others bear terminal sporangia and are therefore fertile (Fig. 656). Telomes also tend to unite into groups, called **syntelomes,** which may be all sterile, all fertile, or mixed. According to this theory the earliest leaves are flattened telomes or **phylloids,** and the sporangium in all cases, together with its stalk or sporangiophore, is a fertile telome. Compound sporangiophores, like those of *Equisetum*, are syntelomes. The phylloids are the prototypes of the microphyllous foliage leaves. In the most primitive condition the sterile and fertile telomes were apparently quite independent of each other. The axillary position which the sporangial telomes occupy in Lycopsida has been arrived at by secondary shifting of the telomes, and Fig. 657 shows three ways in which the change may have taken place. *Equisetum* is assumed to be the product of a line of evolution in which the change did not occur, and consequently it still produces its sporangia independently of its leaves. It must be admitted that it is difficult to accept the idea that the very numerous, closely set and spirally arranged leaves of the *Lycopodium* type have been differentiated from axial structures, and some morphologists

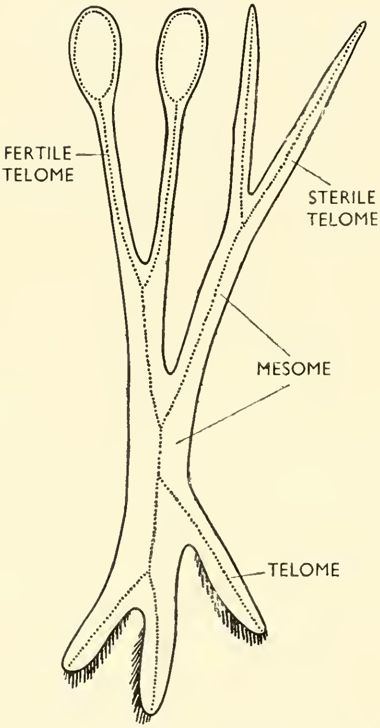

Fig. 656.—Diagram of the organization in a theoretically primitive vascular plant showing a body built of telome and mesome units, the telomes being both fertile and sterile. (*After Zimmermann.*)

maintain that they are merely superficial outgrowths. The evidence is inconclusive and the question must await future solution.

Zimmermann bases his ideas upon simple vascular plants, but we may quite reasonably suppose the sort of differentiation he depicts to have come about at a much earlier stage of evolution, during the development of branching in the primitive algal filament, and to have been carried over directly into the simple vascular body as cortication advanced and the axes grew more massive. Telomes may represent the descendants of the earliest ramuli of the chlorophycean thallus, more massive indeed, but morphologically homologous.

Zimmermann's theory, valuable as it is, nevertheless, stops short of accounting for the origin of the branches or leafy shoots of a higher order, such as are commonly found in all vascular plants even in the simplest Lycopsida. It is clear that all the segments of the original axial system cannot have been reduced, as he suggests, to phylloids or sporangia respectively, both of which are structures of limited growth. Some must have retained the capacity for unlimited apical growth and for the production of fresh telomes. Such a differentiation must have happened, though we can only guess at its mode. The " overtopping " process which established the main axis, would presumably also apply to the branching of the lesser segments or laterals. In their branch systems also one axis would remain predominant, retaining its radial symmetry and apical growth, while the others (telomes of the third order) would be reduced to the specialized appendages of determinate growth, leaves and sporangia.

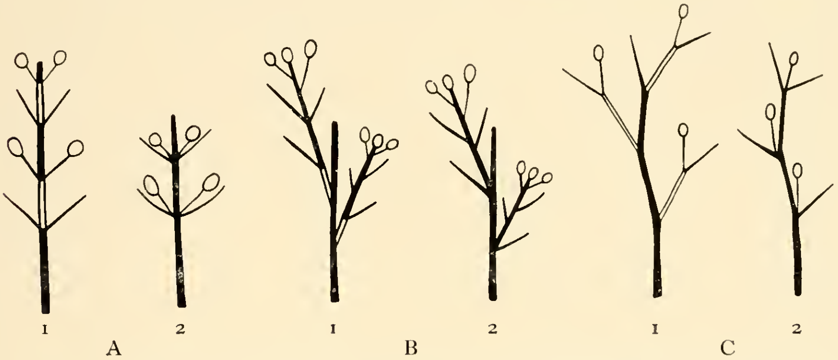

FIG. 657.—Diagram showing three ways in which axillary branching may have been achieved. The portions of the axis which are marked in outline in each case are assumed to have been suppressed. A, 1, Fertile and sterile telomes separated by internodes. A, 2, Alternate internodes suppressed. B, 1, Fertile and sterile telomes on lateral mesomes. B, 2, Basal internode of lateral mesomes suppressed. C, 1, Fertile and sterile telomes in dichotomous pairs. C, 2, Basal internodes of lateral mesomes suppressed. (*After Zimmermann.*)

Whether the still smaller appendages of the plant body, the hairs, spines, glands, etc., which are collectively known as **trichomes,** are derived from very reduced telomes is decidedly doubtful. Many of them originate as direct outgrowths from single surface cells, and there is no line which can be drawn to separate such simple outgrowths from more highly developed trichomes.

The Relationships between Phylloids and Phyllomes

If now we turn to the Ferns we find leaves which are so much larger than phylloids, in relation to the axis which bears them, that they might well be structures of a different order. That this is in fact the case has been suggested by several morphologists, notably Lignier and Tansley. Stripped of detail the theory depicts these large leaves, which dominate the form of the plant, as having evolved from branches of the microphyllous type, complete with their phylloids, so that they are homologous with syntelomes, not with single telomes. Several anatomical facts support this view. Firstly the fern leaf has massive traces, which leave gaps in the stem stele, as we have pointed out above. In this they correspond to the branches rather than to the leaves of Lycopsida, and it is this which has caused them to be labelled megaphyllous. Secondly they show apical growth, sometimes greatly prolonged. Thirdly the leaves of some of the most ancient fossil Ferns have a vascular structure, especially at the base, which closely resembles that of a stem, while in some cases they were not flattened but radially symmetrical. The flattened form and expanded lamina of the fully evolved megaphyllous leaf are supposed to have been produced by broadening and fusion of the phylloids, like the " webbing " of a duck's foot. The amount of fusion which has contributed to the formation of the lamina seems to have varied greatly, and in the most complex pinnate types the pinnules are probably still separate phylloids.

As the original syntelome must have been of the mixed type the sporangia naturally find a place on the megaphyll, and the distinction drawn by Bower between Fern types with marginal and with superficial sporangia may have originated in a difference in the branching of the original syntelome. Possibly the indusium, which is a somewhat late development in evolution, may represent a modified phylloid structure.

The indications are strongly in favour of this view of the megaphyll as the homologue of a branch system, and against the idea that it has developed from the microphyll by simple increase of size. It is a structure of higher order morphologically than the phylloid and is called, distinctively, a **phyllome.** The leaves of all the Spermatophyta agree with this pattern and are phyllosiphonic, which is the justification for Jeffrey's extension of the term Pteropsida to cover everything from the Fern upwards. There is, in fact, no doubt that the Spermatophyta have come from megaphyllous fern-like ancestors, and may be ranked as belonging to the Pteropsida rather than the Lycopsida, in spite of the early evolution of seed-like structures in the latter group.

The root, like the leaf, is no doubt also a specialized portion of the primitive axis. Even in the Liverworts there occur leafless downward extensions of the axis below the ground. This is also found in the Psilopsida and in some Lycopsida, and between these leafless rhizomes and true roots no clear line can be drawn. As is well known, the stelar anatomy of the stem in *Lycopodium* is essentially that of the root in higher plants, which suggests a fundamental unity between the upward and downward phases of the main axis.

Evolutionary morphology thus reduces the cormophyte body to a differentiated system of axes and does away with the presumed fundamental character of the division into stem, root and leaf.

Phytonic Theories of the Shoot

If the leaves, in whatever form they appear, are no more than the elaborated segments of the axis, they may easily be conceived as replacing other axial segments or as combining to form compound axes of a higher order. In the various **Phytonic theories** this is envisaged as happening. The different theories called by this name agree in one essential respect, that they all regard the phyllomes as taking some part in the building of the axes, at least in Spermatophyta. As they are based upon the morphology of higher plants they should be limited to them in their application. Thus restricted many objections to phytonism disappear.

Lotsy summarizes the existing morphological theories of the shoot system as follows:—

1. The stem and leaves are distinct entities, the leaves being appendages of the stem. This was the classic view and is that upheld by Bower's strobilus theory.
2. The shoot is composed of segments, each consisting of a portion of the stem and the leaf belonging to it. This was the original "phyton" theory of Gaudichaud (1841), who regarded the stem as being longitudinally segmented into **phytons**; another form of the theory was suggested by Goethe (1817) and later was adopted by Celakovsky (1901), whose "short segments" or **anaphytes** were transverse units, corresponding to single internodes, with the upper node and leaf in each case.
3. The stem has no separate existence and is composed of the expanded and fused bases of the leaves. This view is associated with Delpino (1883). He described the stem as a **pseudaxis** or phyllopodium and the unit components as **merithalli.**
4. The shoot consists entirely of axial structures, the lateral branches being metamorphosed into leaves. This is essentially the telome theory. Under this heading may also be grouped the **Pericaulome theory** of Potonié (1903), who first proposed the idea of shoot evolution described on p. 647 as "overtopping." His theory goes further, however, in suggesting that the stem in the vascular plants is a compound structure or pericaulome consisting of a primitive axis which has been surrounded by a cortex consisting of the extended bases of the side shoots, now metamorphosed into leaves.
5. The stem is a compound structure consisting of a central axial portion which has been corticated by the extension of the leaf bases around

it in the form of a sheath. This was the view of Hofmeister (1863). It differs from that of Potonié only in its implications, for it accepts the stem and leaf as distinct morphological categories and does not envisage the origin of the central primitive axis by overtopping from a dichotomous thallus.

The **Leaf-skin theory** of Saunders (1922) is essentially similar to that of Hofmeister. It is based on anatomical characters and does not concern itself with evolutionary ideas.

One must recognize that much of the diversity of opinion revealed by the above analysis (Fig. 658) rests upon the acceptance of a too rigid categorization of organs, and the belief, for instance, that a leaf continues to be somehow, mystically, a leaf even when it appears to be part of a stem. Once let us

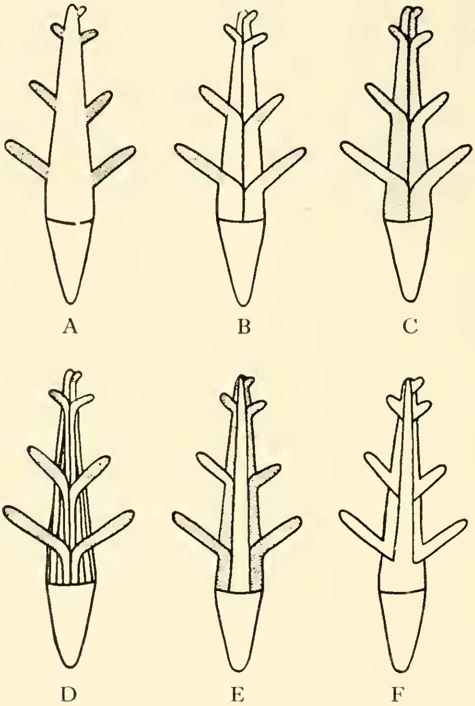

FIG. 658.—Diagram to illustrate various theories of the relationship between leaf and axis in Spermatophyta. Leaf segments stippled, axis segments white. The basal cone represents the primary root. A, The classical view. Leaf and axis as independent categories ; the basis of the strobilar theory. B, The original phytonic view, each leaf growing from a distinct segment of the axis (Celakovsky and Gaudichaud). C, The axis entirely composed of decurrent leaf segments (Delpino). D, The shoot composed of a bundle of axial segments, the terminations of which become leafy. The telome view. E, The shoot contains an axial core surrounded by a sheath of decurrent leaf bases (Hofmeister). F, The shoot contains an axial core surrounded by a " pericaulome " of the bases of lateral branch segments.

accept the idea that all parts of a plant are differentiations from a common structure, a shoot or telome, and the antitheses of the theories are perceived to be false.

The objection urged against all phytonic or segmentation views of the axis, that they necessarily imply a vascular system which is common to stem and leaf and preclude the existence of a true cauline stele, is no longer a difficulty if we accept it as a pointer to a necessary limitation of such theories, namely, that they should be applied only to the Spermatophyta, which alone possess such a common vascular system. The Pteridophyta for the most part show the most definite anatomical evidence of the continuity and unity of the stem as an independent axis, which probably represents a direct derivation from a primordial filament, or **protaxis,** though we may perhaps allow for a peripheral cortication in Potonié's sense, at least in the megaphyllous types. A significant exception is found in the Marattiaceae, in which megaphylly is so pronounced that the stem has become comparatively insignificant and has a vascular system which agrees with that of the Spermatophyta in being of foliar origin.

This may be a clue to the nature of the change of vascular structure which has occurred between Pteridophyta and Spermatophyta. In protaxial structures the axis predominates and the vascular supply to the leaves is dependent on the size of the stem, not on the actual requirements of the leaves themselves. This is ill-adapted, physiologically, to produce a satisfactory balance between supply and demand in the flow of materials to the leaf, a maladjustment which would become more pronounced with the greater extension of the leaves, with the development of the tree habit, and perhaps most of all with the production of leaf-borne seeds, which would make large periodic drafts on the conduction of food reserves to the leaves. The extreme complexity of the stele and the extraordinary development of adventitious roots in tree-like Ferns, both living and fossil, serve to illustrate the difficulties inherent in the protaxial type of plant architecture. The Marattiaceae, on the other hand, show us a way out of the impasse, namely, the contraction of the stem to such a small size that the leaf traces become directly linked to each other and to the vascular system of the roots, forming a common system like that of the Spermatophyta and eliminating the necessity for a cauline stele. Once established, this newer system, which allowed each leaf direct access to the absorptive system, would surely prove more elastic and expansible in the direction of tree-growth than the old. The axis, rebuilt on a vascular skeleton of longitudinally elongated leaf traces, would, however, be no longer a simple structure, but a pseudaxis, as Delpino called it, and such, in the Spermatophyta, it seems to be. One may perhaps go further and suggest that the elimination of centripetal wood, which is known to have taken place during the evolution of the seed plants, accompanied the disappearance of the protaxis or at least the redistribution of its tissues among the component leaf units of the pseudaxis.

No doubt a great part of the theoretical morphology which we have discussed may be criticised as mere speculation, but we would not therefore, as some do, condemn it outright. The mind cannot be restrained from attempting to build for itself a coherent working hypothesis of the unknown, and such imaginative constructions, if they are not allowed to degenerate into dogmas, may sometimes be serviceable guides to investigation.

Summary of Theories regarding the Spermatophyte Shoot

The discussion of the ideas of theoretical morphology which we have attempted in this chapter is necessarily involved and may be difficult at first to follow. It may be useful, therefore, to sum up the main points.

1. The shoot may be interpreted as formed of two distinct categories of organs ; stems and leaves. The latter are regarded under the *Strobilar Theory* as all primitively fertile but subject to progressive sterilization, which eventually limits the fertile zones to the ends of the branches.
2. The shoot may be alternatively regarded under the *Telome Theory* as primitively undifferentiated, composed of leafless axes, the mesomes, bearing terminal segments, the telomes, which may be either sterile or fertile. The body was originally dichotomous, but by a process of overtopping may have become monaxial.
3. According to this second view leaves and sporangia are alike axial structures, both being evolved from the primitive telomes. The axillary position of the sporangia has been arrived at secondarily.
4. While microphyllous leaves, such as those of the Lycopodiales, are regarded as derived from single telomes and are called phylloids, the megaphyllous leaves of Ferns and higher plants are considered as syntelomes, that is, compound structures equivalent to an entire shoot of a microphyllous plant. They are called phyllomes.
5. These phyllomes are believed to have become integrated in the Spermatophyta into sympodia which have replaced the original axis by a compound structure. The various views as to the nature of this compound axis are called phytonic theories. According to the interpretation here advanced, such views are only applicable, if at all, to the Spermatophyta, while in all the Vascular Cryptogams, except possibly the Marattiaceae, the axis is regarded as representing the primitive mesomes of the earliest land plants, that is to say, structures which may be ultimately traceable to the cellular filaments of primitive Thallophyta.

CHAPTER XVII

THE GYMNOSPERMAE: CONIFERALES AND TAXALES, THE PINES AND YEWS

THE Gymnospermae include the simpler members of the Spermatophyta and form, as it were, a bridge between the Pteridophyta on the one hand, and the Angiospermae on the other. They are more ancient than the Angiosperms and in their method of reproduction they show indications whereby we can recognize the way in which the Angiospermic flower may have evolved, though this does not imply that any living Gymnosperm can be regarded as an ancestor of the Angiosperms.

The group includes the Pines and Yews, together with a number of less known groups, for example the Cycadales, the Ginkgoales and the Gnetales, the latter having certain characters in common with the Angiospermae.

In the Gymnosperms, as in the Angiosperms, the reproductive organs are aggregated into flowers, but these differ considerably from those of the higher Flowering Plants. In the Angiosperms the female reproductive organ or **ovule** is enclosed in a special protecting structure, the **carpel,** which forms a closed ovary. In the Gymnosperms the ovules are borne exposed on sporophyllous scales. Hence the term Gymnospermae or " naked seeds " has been given to this group.

The most important order of the Gymnosperms is the Coniferales, which includes Pines, Spruces, Firs, Larches, Cypresses and Araucarias. They are mostly evergreen trees, though a few, like the Larch, lose their leaves in winter, while some, like the Juniper, seldom attain the size of trees. Most of the Conifers grow in relatively dry, poor soils, and the leaves show modifications which enable them to combat these arid conditions. Plants which live in dry habitats are termed **xerophytes,** and one of the characteristics of such plants is that the leaves are usually small and so constructed as to expose a reduced surface to the drying action of the atmosphere. This is true of the majority of the Conifers, in which the leaves, or " needles " as they are popularly called, are very narrow and resemble in appearance small green shoots.

In this respect the Conifers differ markedly from the Cycads in which the leaves are very large and are more like those of the Ferns. In fact in the Gymnosperms we have two main structural types, the one exhibited by the Conifers, with much branching and small leaves, the other typified by the Cycads with few branches and large leaves. A marked difference in the stem anatomy exists between the tree-like Conifers and the shrub-like Cycads. The wood in the first type is dense and massive and has been called

pycnoxylic, while in the latter case it is **manoxylic,** that is to say, loose, soft and scanty, as in many of the Pteridosperms.

The flowers take the form of cones made up of **cone scales.** In the Conifers these are relatively small except in a few cases, but in the Cycads the cones are very large, often a foot or more in length. These cones are made up of an aggregation of sporophylls bearing sporangia in which the spores are produced. The cones are generally unisexual, the male being borne separately from the female, and frequently differing from it considerably in shape and size. Hermaphrodite cones sometimes occur as abnormalities. The female cones are long-lived structures, sometimes remaining on the plants for several years before they become mature and the seeds are ripened. The male cones are usually smaller and short-lived.

The gametophyte generation is even more reduced than it is in any of the Pteridophyta. Neither the male nor the female gametophyte ever possesses an independent existence, and the male prothallus is represented only by one or two cells.

The Gymnospermae are divided into a number of orders, some of which are represented only by fossil types. Others possess both fossil and living forms, but the general indications are that the highest development of the Gymnosperms was during the Jurassic period, and that the present-day forms are the remains of a more numerous fossil group.

The following are the orders generally recognized :—

1. **Cordaitales,** *e.g.*, *Cordaites* (fossil).
2. **Coniferales,** *e.g.*, *Pinus.*
3. **Taxales,** *e.g.*, *Taxus.*
4. **Cycadales,** *e.g.*, *Cycas.*
5. **Bennettitales,** *e.g.*, *Cycadeoidea* (fossil).
6. **Ginkgoales,** *e.g.*, *Ginkgo.*
7. **Gnetales,** *e.g.*, *Ephedra*, *Gnetum*, *Welwitschia.*

The type genus, which will be described in detail, is given in each case, except for Cordaitales and Bennettitales, which will be dealt with in Volume III.

The order of the groups given above is that in which they will be treated in this book, which is dictated by considerations of convenience of description and teaching. It does not represent a phylogenetic sequence, since in this respect the Cycadales and Ginkgoales would rank as primitive types among the living Gymnosperms.

Coniferales

This is much the largest order of the Gymnospermae. Its members are nearly all evergreen trees or shrubs and include the giant Redwoods of California (*Sequoia*), the largest trees in the world. Representatives of the group are to be found in every country, but they reach their greatest development in the northern hemisphere, especially in the colder zones of Canada, Scandinavia, Russia and Siberia, where the Pines and Firs reach to the northern limit of tree growth and probably cover a larger land area than any other group of plants. Their leaves are usually either linear and needle-like or else form green scales closely appressed to the stem. They may be either whorled or spiral in their arrangement on the shoots. A few, like the Monkey Puzzle (*Araucaria imbricata*), have broad leaves, but share the same hard, cuticularized texture characteristic of the needle leaves. This leathery consistency of the leaves is associated with anatomical characters which point to a need for the conservation of water.

The arrangement of the genera of Coniferales has not reached stability. A number of sub-orders are recognized, but their limits and the genera assigned to them vary with different authors. The inclusion of the Yews in the order is also uncertain, and we here adopt the view that they should form a separate order, the Taxales. The leading characteristics of most of the sub-orders are, however, fairly clear and are given below with the principal genera assigned to them.

Araucariineae. Broad-leaved trees with very large cones; mostly in Australasia and South America. The ovuliferous scales are mostly completely fused to the sporophylls, the free end being sometimes called a ligule. The male gametophyte has many prothallial cells and the female many archegonia, which is usually looked upon as a primitive character. The chief genera are *Araucaria* and *Agathis*.

Podocarpineae. Small trees, mostly in the Southern Hemisphere. There are no female cones, the female flowers being borne singly in the axils of bracts and containing only one anatropous ovule, which surmounts a fleshy pedestal composed of the fused tissues of its stalk and of the bract. The chief genera are *Podocarpus*, *Saxegothaea* and *Dacrydium*.

Abietineae. Large trees with narrow or needle-like leaves, often borne on foliar spurs. In the female cone the bract is free from the ovuliferous scale, which is usually considerably the larger of the two. Mostly North Temperate in distribution. The chief genera are *Pinus*, *Picea*, *Larix*, *Abies* and *Cedrus*.

Taxodineae. Large trees with narrow or spine-like leaves. In the female cone the bract is almost completely united to the ovuliferous scale, only the double end showing the composite nature of the combined structure. The chief genera are *Taxodium*, *Sequoia*, *Sciadopitys* and *Cryptomeria*.

Cupressineae. Trees varying from very large size to mere shrubs. Leaves usually small, often closely appressed to the branches and even fused to the latter and to each other. Female cones small, the scales simple, somewhat fleshy and only the upper ones fertile, larger than the others and each bearing a number of erect ovules. Fertile scales sometimes fused together at maturity. The chief genera are *Cupressus*, *Thuja*, *Callitris* and *Juniperus*.

Pinus sylvestris (The Scots Pine)

The genus *Pinus* includes about seventy-five species at present living. Geologically its history does not go back beyond the Jurassic period, though pollen grains which might be those of *Pinus* have been found in Triassic rocks.

Fossil wood known as *Pityoxylon*, which is essentially similar to pine wood, can be traced back to the Carboniferous times, so that a direct connection of *Pinus* with the Cordaitales is not improbable.

The Scots Pine is frequently found growing in this country, where it forms a tall forest tree up to 100 ft. high (Fig. 659). Although at the present day it is only truly native in Scotland, so far as Britain is concerned, it was formerly native in England, and has been extensively planted since the eighteenth century.

Native Pines generally grow gregariously, forming rather open forests. Isolated specimens are sometimes seen, especially on wind-swept heights, where their original shape is frequently altered by the influence of the prevailing wind and they become dwarfed and bent. Only a few scattered remains of the great Caledonian Pine forest are to be found in the Scottish Highlands, which were densely forested in former ages, as Scandinavia is to-day.

FIG. 659.—*Pinus sylvestris.* In Langdale, Cumberland.

The tree possesses a **tap root** growing straight down into the soil, but in most examples this tap root disappears at an early stage and is replaced by **lateral roots,** which form a massive root system. It may be that this is partly accounted for by the fact that the tree frequently grows on shallow soil overlyng rock where it would be impossible for a tap root to penetrate. In any case we generally find that the rooting system of the Pine is spread out over a large area, but that none of the roots penetrates very deeply into the soil.

The main stem is cylindrical and is covered with a very rugged, scaly bark. The stem branches monopodially, forming lateral branches in whorls from buds developed in the axils of scale leaves at the end of each year's growth. This regular development of branches gives the young tree a very symmetrical appearance, but in old specimens the symmetry is lost by the death of the lower branches, and the irregular growth of the remainder. The tree then assumes the familiar umbrella form. The scars marking the position of the lost whorls of branches can be seen on the main trunk of the old tree and give a useful indication of its age.

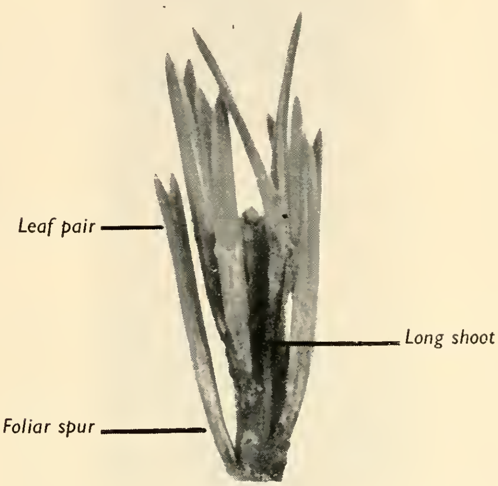

Fig. 660.—*Pinus sylvestris.* Young branch showing foliar spurs bearing paired leaves.

In monopodial branching the main stem continues indefinitely in active growth as the leading shoot. If this is accidentally destroyed there is a most interesting " struggle for precedence " which Errera has described. Two or more of the uppermost lateral branches assume the vertical position and a competition for leadership ensues. When the strongest of these shoots has asserted its dominance it replaces the missing leader and the others fall back into the lateral position again.

In addition to the branches which have unlimited apical growth there are very numerous " dwarf shoots " or **foliar spurs** of limited growth, which arise in the axils of scale leaves borne on the main branches (Fig. 660). The leaves are of two kinds. Firstly there are the **foliage leaves** or " needles " which appear only on the foliar spurs. The number of such leaves produced on a spur may be one, two, three or five according to the species, but in *Pinus sylvestris* there are only two. The leaves have a smooth surface and deeply sunken stomata, which are characteristic of xeromorphic types. The second kind of leaf, termed the **scale leaf,** is developed as a protective structure. These leaves are borne both on the main branches and also on the foliar spurs and fall off as the branches mature. They are brown in colour and are not capable of assimilation. Their function appears to be to assist in the conservation of moisture around the branches.

The Pine is an evergreen, that is to say, it does not shed all its leaves at the same time. The foliage leaves persist for a number of years and only fall when the spur is shed as a whole.

Trees with no lower branches and with trunks without " knots " are of special value for timber, and it is for this reason that it is customary to plant Pines very close together so that the tendency to produce lateral branches is repressed. Pine wood forms the " Deal " of commerce and is used in very great quantities both in building construction and in making cheap furniture. It is also employed almost exclusively for pit props in coal mines and as wood pulp in paper manufacture.

Anatomy of the Stem

The anatomy of the stem resembles that of a dicotyledonous Angiosperm, though on the whole it is simpler. The growing point is an obtuse cone of

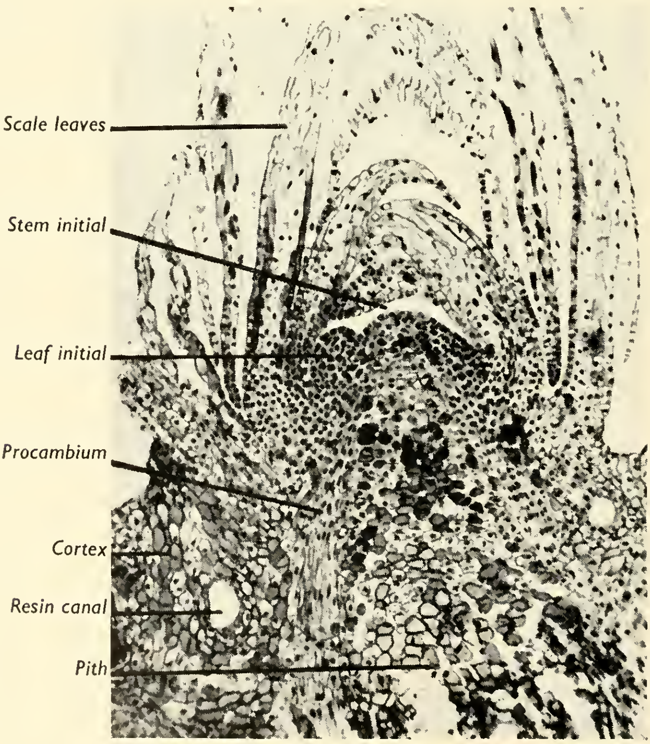

Fig. 661.—*Pinus sylvestris.* Longitudinal section through the growing point of a long shoot.

meristematic cells, the apex of which is occupied by an actively dividing group of initial cells (Fig. 661). From these are derived two zones of tissue, a central zone of large, pith-forming cells and an outer zone which corresponds morphologically to the tunica (see p. 850), although its cells do not only divide anticlinally. In this outer zone there arise a number of **procambial strands,** in which certain radial rows of cells become differentiated into **protoxylem** and **protophloem** at their inner and outer ends respectively. At a later stage the median band of undifferentiated procambial cells in each strand becomes the **cambium,** from which **metaxylem** is formed internally and **metaphloem** externally. All these together constitute a **vascular bundle** of **primary xylem, cambium** and **primary phloem.**

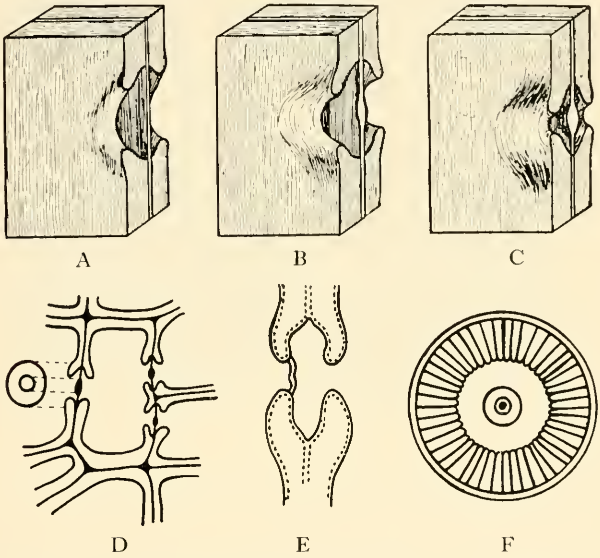

FIG. 662.—*Pinus sylvestris.* Bordered pits. A, B and C, Stages in the growth of border and torus in three-dimensional view. D, Bordered pits in transverse section. E, Bordered pit with torus displaced laterally, filling aperture of pit. F, Pit membrane in surface view with central torus and radial striations. (*After Stevens.*)

The walls of the protoxylem elements show a loosely spiral thickening with a few small **bordered pits.** The metaxylem elements are thickened with either a close spiral or a close reticulum, while the bordered pits become larger and more numerous in the later formed elements.

A bordered pit is a circular area of unthickened middle lamella, which is over-arched on each side by a dome formed of the inner, lignified layer of the cell wall (Fig. 662). Each dome has a small central opening. On the lamella, and in line between the two openings, there is a small disc of lignin called the **torus,** around which radiate a number of openings in the lamella, like the spokes of a wheel. The torus acts as a stopper, for any marked drop of pressure on one side of the pit will draw the lamella over to that side, where it lies in contact with the dome, the torus fitting over and stopping up the opening on that side and thus saving the membrane from rupture.

The woody tissue of *Pinus* contains predominantly only one type of conducting cell, the **tracheid,** though the primary and secondary tracheids differ in the pattern of their thickening, but in the earliest primary xylem there are very long spiral elements which appear to be true vessels. If this is the case their absence from the mature wood is a matter of some evolutionary interest.

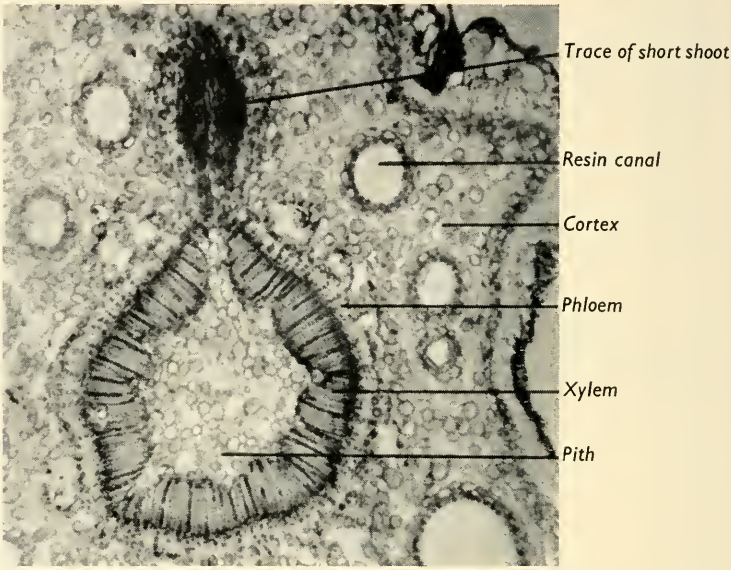

Fig. 663.—*Pinus sylvestris.* Transverse section of a young branch showing an early stage in secondary thickening.

As each tracheid is a closed cell, the water passing through the stem must traverse thousands of bordered pits on its way, and their aggregate resistance to the flow must be considerable. The reduced size and sclerotic character of the leaves have often been attributed to this resistance in the xylem, limiting the water supply to the foliage. Measurements made by Farmer of the relative conductivity of woods in many species bear this out. The conductivity of Conifer wood averages about one-half that of evergreen Angiosperms and less than one-quarter that of deciduous Angiosperms, that is to say, those which drop their leaves in winter.

The protophloem is soon crushed out of existence by the pressure of the growing tissues. The metaphloem consists of short **sieve tubes** with sieve plates on their radial longitudinal walls and a few on their oblique end-walls. Phloem parenchyma cells are also formed, but no companion cells.

Between the primary bundles are the parenchymatous **primary medullary**

rays, connecting the **pith** with the external **cortex.** No pericycle or endodermis can be seen. Outside each bundle there is a large **resin canal** in the cortex. The outer surface is covered by a very highly thickened **epidermis,** beneath which is an equally thickened **hypodermis.**

The fully formed cambium consists of a single layer of meristematic cells, which repeatedly divide in a tangential direction. Of the two cells thus formed at each division one remains cambial, the other, the tissue mother cell, divides again tangentially and the two cells thus formed become transformed into either xylem cells or phloem cells respectively, according to whether they lie on the inside or the outside of the cambial cell. Exceptionally there may be more than one division of the tissue mother cell, so that three or even four cells may be added to the vascular tissue from one tissue mother cell. Certain cambial cells produce only parenchymatous cells, which form radial rows dividing the tissues of the bundle. By this means portions of the primary bundle are separated off on each side and these portions pass out through the cortex as the **leaf traces** of the scale leaves.

The cambium also extends itself tangentially, so that the bundles gradually increase in width (see Fig. 663), narrowing down the primary medullary rays until neighbouring bundles make contact and close the ring. This brings the edges of the bundle cambia together, and from this point we may date the so-called **secondary thickening,** which develops a closed ring of vascular tissues. It is well to emphasize, however, that there is no real discontinuity between the primary and the secondary growth.

The cambium having now formed a closed ring, its further development produces a continuous zone of **secondary xylem** on the inner side and one of **secondary phloem** on the outer side (Fig. 664). At many points these two zones are traversed by **secondary medullary rays,** also produced from the cambial cells, to replace the primary rays. They are mostly uniseriate, that is, they are only one cell broad and they are usually less than a dozen cells in height (Fig. 665). They are composed of rectangular cells with thick walls and numerous simple pits, but each contains cytoplasm and a nucleus, with many starch grains. The upper and lower margins of the rays are formed of one or two rows of **marginal ray-tracheids,** running horizontally, but otherwise resembling short tracheids of the xylem, from which they may be derived (Fig. 666). In the cambium and phloem zones these marginal tracheids are replaced by large, thin-walled cells which extend upwards and downwards between the cells of the vascular tissue. They contain much free protein and are apparently storage cells, like the starch-storing cells of other parts of the ray. These are sometimes referred to as **albuminous cells.**

Each successive year new medullary rays are formed, between those previously laid down, thus, as the distance from the centre increases, the average distance between adjacent rays remains approximately the same.

The areas of contact between medullary ray cells and tracheids of the wood are called the **ray fields.** Each is marked by a large thin area or simple pit, which is in striking contrast with the bordered pits that connect the tracheids with each other.

The secondary wood is also made up of tracheids which are about 4 mm.

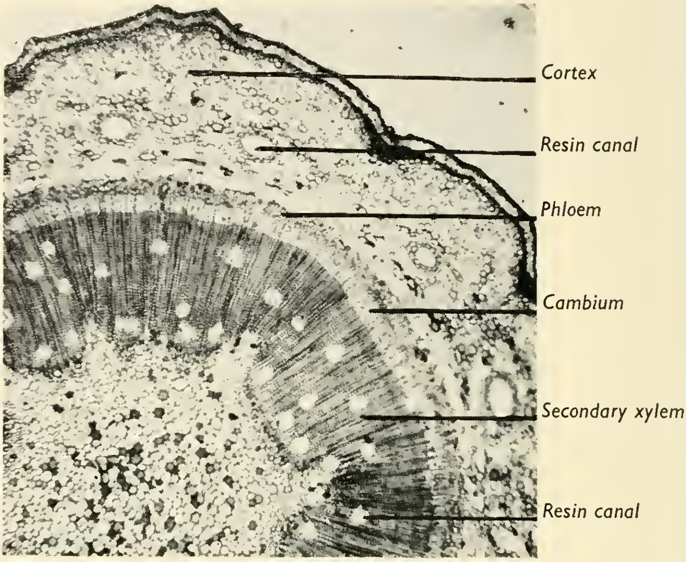

FIG. 664.—*Pinus sylvestris.* Transverse section of a branch showing secondary wood containing resin canals.

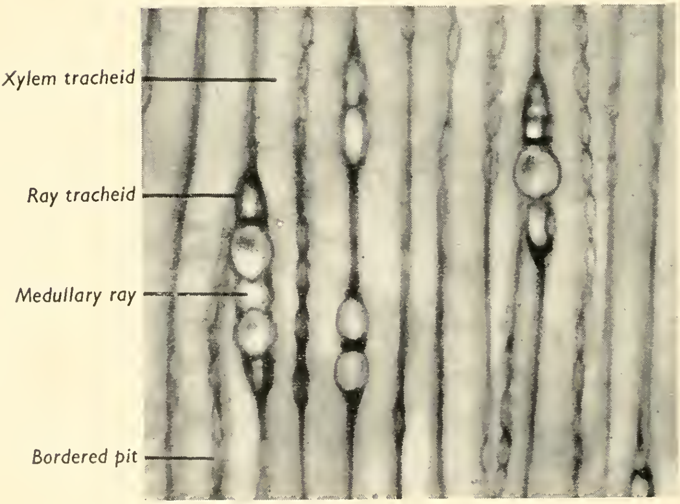

FIG. 665.—*Pinus sylvestris.* Longitudinal tangential section of the secondary wood showing medullary rays and bordered pits on the radial walls only of the tracheids.

long and pointed at both ends. They are almost square in section, and their radial walls are marked by a single row of large bordered pits.

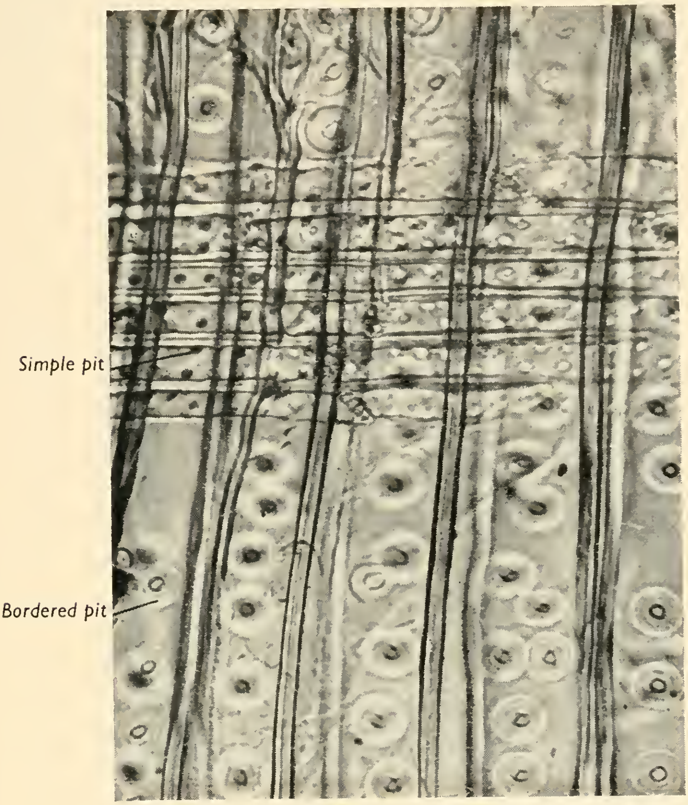

FIG. 666.—*Pinus sylvestris*. Longitudinal radial section of the secondary wood showing bordered pits on the tracheids and small simple pits in the medullary ray. The medullary ray is cut longitudinally and is seen crossing the tracheids in a horizontal direction.

The wood is not uniform throughout, for in transverse section it is possible to recognize rings, termed **annual rings,** each of which represents a year's growth (Fig. 667). The occurrence of these rings can be explained if we realize that the size of the tracheids produced in the autumn, when the supply of food material is slowing down, is smaller than that of those produced in the spring, when with the first burst of activity large quantities of food material are available and larger tracheids are laid down. Counting the number of such rings gives an estimate of the age of the tree or branch.

The walls of the autumn tracheids are much thicker than those in the spring wood and their walls show a spiral striation of fine lines. The openings of their bordered pits are not circular but narrowly elliptical and lie at right angles on opposite sides of the wall, so that each pit, in surface view, seems to be marked with a cross. The last row of tracheids in each annual ring is peculiar in having pits on its tangential walls as well as on the radial walls, thus ensuring continuity between successive rings.

The secondary phloem is made up largely of radial rows of sieve tubes with many lateral sieve areas, on the radial walls, which become covered with callus after their first year. Some scattered parenchyma cells are also present.

So far we have only considered the structure of the stele ; we must now turn to the cortex. In the very young stem the cortex is made up of parenchymatous cells, and since the endodermis and pericycle, if present, are composed of the same type of cells it is impossible to recognize them as separate layers. As growth continues, a layer of cortical cells near the outside becomes active and forms a meristematic layer termed the **cork cambium** or **phellogen.** This layer cuts off additional cortical cells towards the inside and **periderm** or **cork** towards the outside. This cork layer, which constitutes the **bark,** is impervious to water and serves to protect the stem from excessive evaporation. It also provides a protection to the more delicate tissues within.

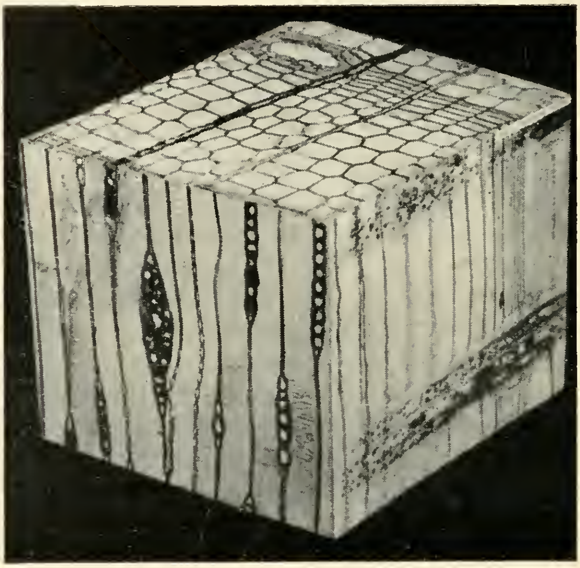

Fig. 667.—*Pinus sylvestris.* Three-dimensional model of a block of wood showing one annual ring with wide tracheids in the spring wood and narrow tracheids in the autumn wood. The medullary rays are also seen in transverse and longitudinal views. (*From a model in the National Museum of Wales.*)

All these structures are also found in the stem of the Angiosperms, and we shall consider them again in more detail when we come to study the anatomy of that group. In *Pinus* and in many other Conifers belonging to the Abietineae large **resin canals** are present in the cortex opposite each primary vascular bundle, and small canals form a connected system throughout the wood and the phloem. They also run horizontally along many of the medullary rays. These ray canals have been traced continuously through more than a hundred annual rings, but however long they are, they always begin where a ray touches a vertical canal. This system of resin canals or passages is occasionally met with in the higher plants, for example, in the Ivy, but it is more characteristic of the Conifers. Each canal is bounded by a layer of glandular secreting cells called an **epithelium** (Fig. 668). The canals contain Turpentine, which flows out when any injury breaks the tissues open. The Pines have very little power of forming callus tissue over wounds, so that the antiseptic action of the Turpentine is valuable as a protection against the invasion of the wounded tissues by Fungi or Bacteria. When exposed to the air the Turpentine is oxidized to solid Resin which remains as a covering to the wound until fresh bark can be formed. Distillation of Pine wood, leaves, etc., is the chief source of natural Turpentine. The resin canals of *Pinus* are sometimes blocked by the ingrowth of epithelial cells, forming vesicles called **tyloses.** This apparently occurs as a result of injury. In *Cedrus* there are normally no resin canals, but they occasionally appear where the wood has been damaged. Jeffrey has claimed that the production of anomalous structures as a result of injury throws light on the evolutionary history of the species and has raised it to a principle under the name of "traumatic reversion," an idea of doubtful significance. The example quoted, if interpreted in this manner, would suggest that *Cedrus* was derived from ancestors which had formerly possessed resin canals.

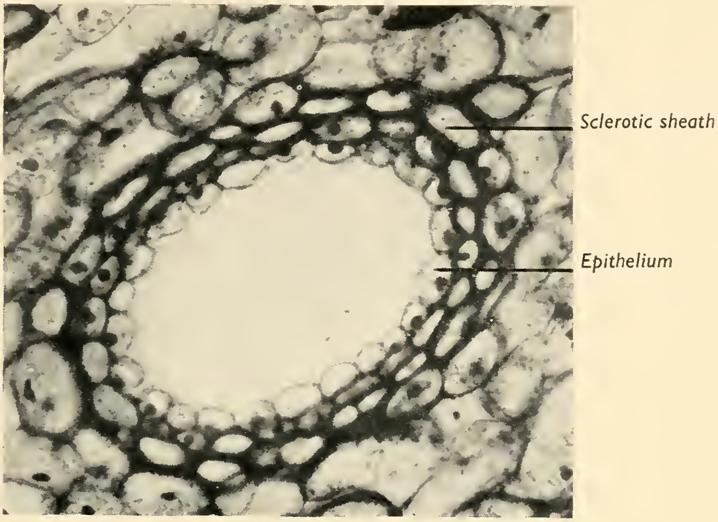

FIG. 668.—*Pinus sylvestris.* Transverse section of schizogenous resin canal in the cortex, with lining epithelium and sclerotic sheath.

Anatomy of the Root

The root of the Pine resembles that of a Dicotyledon, but it is on the whole simpler. The apical meristem produces no leaves, and it also differs from that of the stem in cutting off a series of cells forwards as well as backwards. These cells are short-lived, but they form the protective **root cap,** which acts as a buffer between the delicate cells of the meristem and the hard particles of the soil. The young root is clothed with a zone of short **root hairs,** which are thin-walled prolongations of the cells of the external or **piliferous layer.** The root hairs in the Conifers are not well developed and soon disappear. Within the piliferous layer is a wide zone of parenchymatous cortex which is bounded on the inside by the **endodermis.** This layer is composed of suberized cells, usually impregnated with tannin which gives them a brownish orange colour.

The stele is limited by the **pericycle,** which may consist of six or more layers of cells, which are also frequently impregnated with tannin and contain starch grains. There are generally two protoxylem groups, which lie at the ends of an ellipse of metaxylem in the centre of the root. The development of this metaxylem proceeds from the two protoxylem groups towards the centre, so that in a very young root some of the central cells may still be found unlignified. The phloem forms two arcs, on each side of the metaxylem, and separated from it by parenchymatous cells. This separation of the xylem and phloem is characteristic of root structure in general. Each protoxylem group is slightly forked, formed a Y, and between the branches lies a large resin canal.

Often, even before the primary tissues have been completely organized, secondary thickening begins by the development of a cambium from the parenchymatous cells between the phloem and the metaxylem (Fig. 669). This cambium cuts off secondary xylem towards the centre and secondary phloem towards the outside, so that two masses of secondary tissue are formed, separated by two wide medullary rays, one opposite each protoxylem. Later the cambium extends itself across these rays, outside the resin canal, and the extension of the secondary wood gradually encroaches on the primary rays until they are reduced, in the course of one or two annual rings, to the width of a single cell, when they become indistinguishable from the secondary rays.

As soon as the cambium has become active a layer of the pericycle commences to function as a **cork cambium,** and cuts off a layer of cork cells towards the exterior. As this process continues a thick layer of cork is formed separating the cortex from the stele, and thus being deprived of food by this barrier of cork, the cortex soon dies and disappears. From the beginning of cork formation the older part of the root ceases to be an organ of absorption and functions only as a conductor of watery material absorbed by the young, actively growing end of the root.

Although generally there are only two protoxylem groups in the root of the Pine, when it is said to be **diarch,** occasionally three are found, when the root is spoken of as **triarch,** and higher numbers, up to six occur.

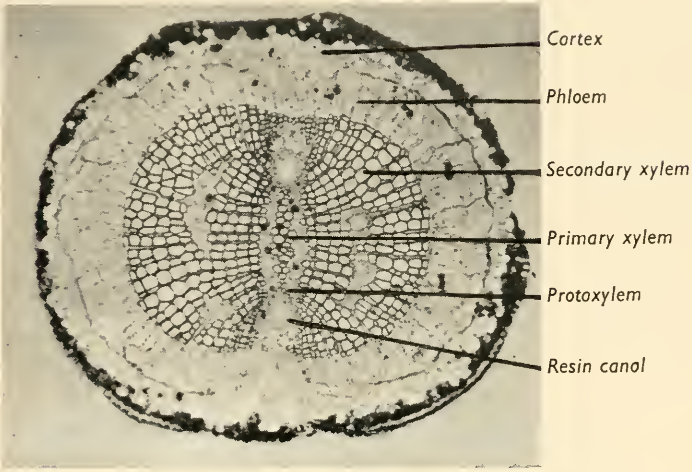

Fig. 669.—*Pinus sylvestris.* Transverse section of young diarch root showing the primary xylem plate separated from the secondary wood by a zone of parenchymatous cells. A resin canal lies opposite each protoxylem in the primary medullary rays.

The younger roots of the Pine are commonly invested by fungal hyphae which form a complete layer over the surface. This is called an **ectotrophic mycorrhiza.** Great importance has been attached to this association in regard to the nutrition of the tree (Fig. 670) (see Volume IV).

Fig. 670.—*Pinus sylvestris.* Rootlets invested with mycorrhizal fungus, seen by dark-ground illumination.

Anatomy of the Leaf.

In a transverse section of the leaf we find a specialized structure different from that obtaining either in the leaves of the Cryptogams or in the typical leaf of the Angiosperm (Fig. 671). The whole anatomy suggests strict conservation of the water supplies, and it is therefore spoken of as **xeromorphic.**

The leaves are semicircular in cross-section, each pair having their flat surfaces facing each other. Bounding the outside of the leaf is a very thick-walled **epidermis.** This is covered on the outside by a thick **cuticle. Stomata** are developed in longitudinal rows, on all sides of the leaf, and the **guard cells** are sunken in grooves, well below the general surface of the epidermis.

Beneath the epidermis is a **hypodermis,** composed of one or two layers of sclerenchymatous cells, interrupted by air spaces below each stoma. The parenchymatous **mesophyll** is not divisible into palisade and spongy tissue, but is made up of thin-walled cells, containing numerous chloroplasts and rich in starch, whose walls show numerous infoldings, which project into the cavities of the cells.

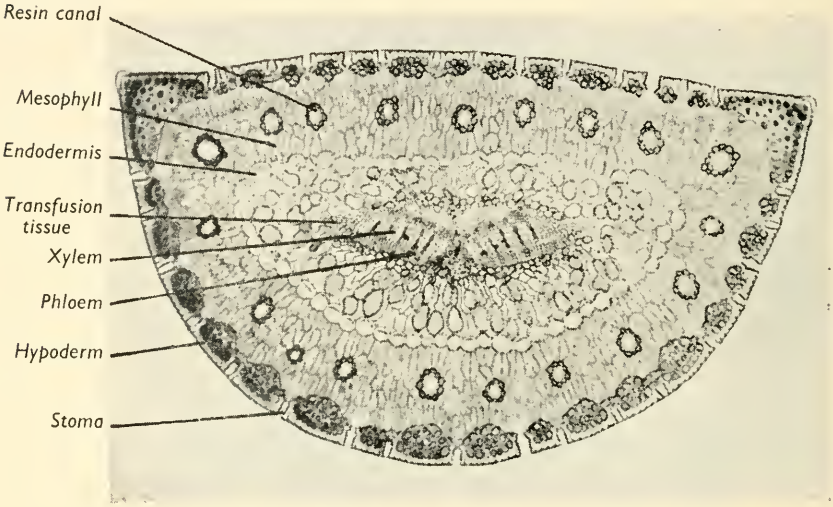

FIG. 671.—*Pinus Sylvestris.* Transverse section of a needle leaf. The flat side is adaxial.

These curious folds run in a circular manner round the cell and represent rigid, non-growing, ring-like zones in the wall. When they are formed the further growth of the cell causes the softer wall portions between the rings to bulge out in balloon-like expansions, whose sides, in contact with each other, give the appearance of folds. There is thus no actual inward growth of the cell wall, which would have to be against the turgor pressure in the cell and would be difficult to understand. Around the outer part of the leaf is a ring of **resin canals** similar in structure to those of the stem.

In the centre of the leaf is a well-marked **endodermis** surrounding a many-layered **pericycle,** within which are two vascular bundles, which run closely parallel and unbranched from base to apex of the leaf. These two bundles arise from a single leaf trace, and in some Pines the trace continues single throughout the leaf. The pericycle is made up of a number of types of cells. Firstly, there are parenchymatous cells rich in proteins, which are called **albuminous cells**; they abut upon the phloems of the vascular bundles. Secondly, there are cells with bordered pits and no contents, which are termed **tracheidal cells**; they lie alongside the bundle xylems. Thirdly, there is typical parenchyma in which these two types of cells are embedded. These special tissues are called collectively the **transfusion tissue**. This is characteristic of the leaves of Conifers and apparently assists in the diffusion of fluids to and from the mesophyll. Probably it makes up for the poor development of vascular bundles in the leaf.

The apparent absence of any intercellular spaces in the mesophyll, as seen in transverse section, is explained when a longitudinal section is examined (Fig. 672). Then we see that the mesophyll consists of transverse plates of cells, one cell thick, and that the plates are separated, sandwich fashion, by spaces which run right across the leaf and provide adequately for the circulation of air to the mesophyll cells.

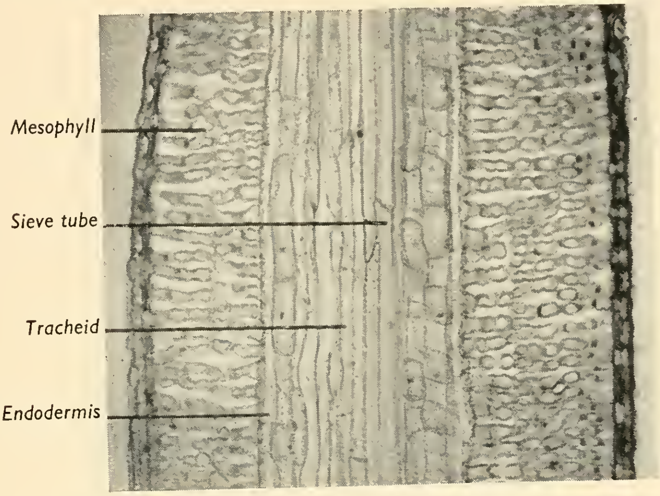

FIG. 672.—*Pinus sylvestris*. Longitudinal section of leaf showing the lamellar structure of the mesophyll.

REPRODUCTIVE ORGANS

The reproductive organs consist of spores which are produced in sporangia, borne on specialized structures which are at least partly sporophyll in nature and are aggregated together into the cones. Although these structures are sporophytic in origin and therefore cannot be regarded as being in any way sexual in character, it is customary to refer to them as male and female cones. The **male cones** are borne in clusters at the base of the youngest shoots. They appear in the early spring and produce microsporangia in which microspores are formed. These microspores are equivalent to the **pollen grains** of the Angiosperms.

The **female cone,** which takes three years to develop, is a more substantial structure, consisting of a woody, central axis bearing lateral appendages in a close spiral. These bear the megasporangia in which are developed the megaspores.

THE MALE CONE

The male cone is produced in the axil of a scale leaf at the base of the developing shoot of the current year, and thus replaces a short shoot (Fig. 673). It consists of an axis about 5 mm. long, at the base of which are a number of small scales, above which are arranged, spirally, between sixty and one hundred specialised leaves or **microsporophylls.** In longitudinal section it is seen that each sporophyll arises from the central axis (Fig. 674) and passes out horizontally to terminate in a flattened head, part of which projects upwards and overlaps the sporophyll above, while part turns down and covers the two **microsporangia** or pollen sacs, which are attached along the under side of the sporophyll. A single vascular bundle enters the sporophyll but stops short before reaching the head.

FIG. 673.—*Pinus sylvestris.* Young shoot bearing a group of male cones.

Within the wall of the sporangium we can recognize at an early stage a peripheral **tapetum** and a central **archesporial** tissue. From the latter a number of **microspore mother cells** are differentiated. The nucleus of each divides twice, meiotically, whereby the chromosome number is halved. Thus from each mother cell four **microspores** are produced, each of which possesses the monoploid chromosome number. These microspores or pollen grains separate from one another and are nourished by the absorption of materials from the tapetal cells, which disintegrate as the spores ripen.

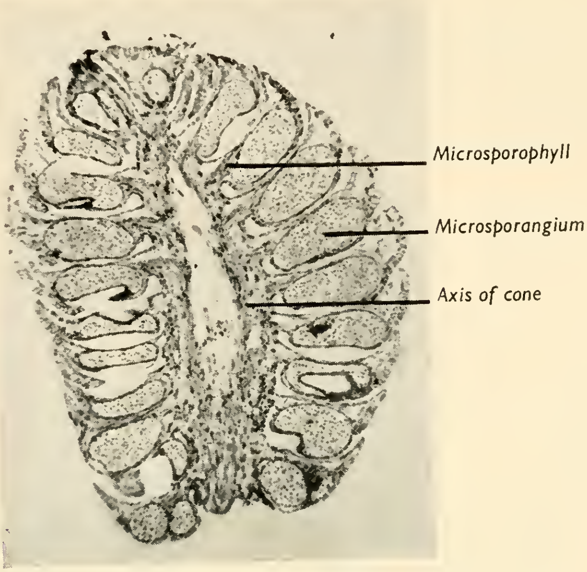

Fig. 674.—*Pinus sylvestris.* Longitudinal section of the male cone showing the spirally arranged microsporophylls with attached sporangia.

The microspore is at first a unicellular body covered with a three-layered coat. The outer layer, or **extine,** is heavily cuticularized, but it does not completely cover the mature spore and is found only on one side, the rest of the spore being covered by the exposed middle layer, or **exo-intine.** This layer is distended into two large **air sacs,** which greatly increase the buoyancy of the spore and aid in its dispersal by wind. The inner layer or **intine** is very thin (Fig. 675).

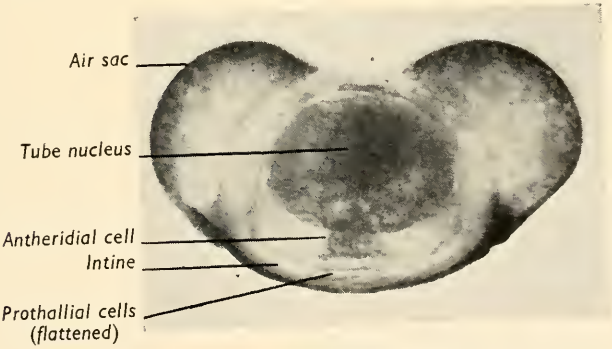

Fig. 675.—*Pinus sylvestris.* Mature microspore in optical section.

The nucleus of the microspore first divides into two and a wall is laid down between them dividing the body of the spore into a very small **prothallus cell** and a large portion called the **tube cell** because it later develops into the **pollen tube.** The prothallus cell is flattened against the cell wall and rapidly disorganizes, being overlaid by a thickening of the intine.

Shortly after this stage the spores are shed by the bursting of the wall of the sporangium along its under side. This occurs in May. When the sporangia are empty the cone rapidly withers and drops off.

The Female Cone

The female cones are developed laterally in the axils of scale leaves. They are usually produced in clusters in place of shoots of unlimited growth and on different branches from the male cones. They begin to develop during the winter and are ready for pollination in the following spring (Fig. 676).

Fig. 676.—*Pinus sylvestris.* Terminal portions of branches with young female cones in spring (left) and summer (right) of their first year.

The young female cone is small and reddish in colour, and like the male cone consists of a central axis bearing outgrowths which are arranged spirally, those at the base being smaller and sterile. Each of these outgrowths is made up of two structures, the smaller of which is spoken of as the **bract scale,** which is directly connected to the central axis, and the larger, the **ovuliferous scale,** which develops on the upper surface of the bract scale (Fig. 677). The bract scale is leathery and the ovuliferous scale is woody. The latter is wedge-shaped, with its broad end outwards, and it develops so as to conceal the bract scale from view. The outer surface of the cone consists of the rhomboidal ends of the ovuliferous scales, each with a small central point or **umbo.**

This double structure has long been a morphological puzzle. The ovuliferous scale is supplied by a vascular trace which arises quite independently from that of the bract scale, and it is held by most botanists to be axillary to the bract scale and therefore a branch or part of a branch. If the bract scale is homologous with a scale leaf of the vegetative shoots, then the ovuliferous scale must be homologous with a modified leaf spur. Its vascular structure, however, is rather that of a leaf than an axis.

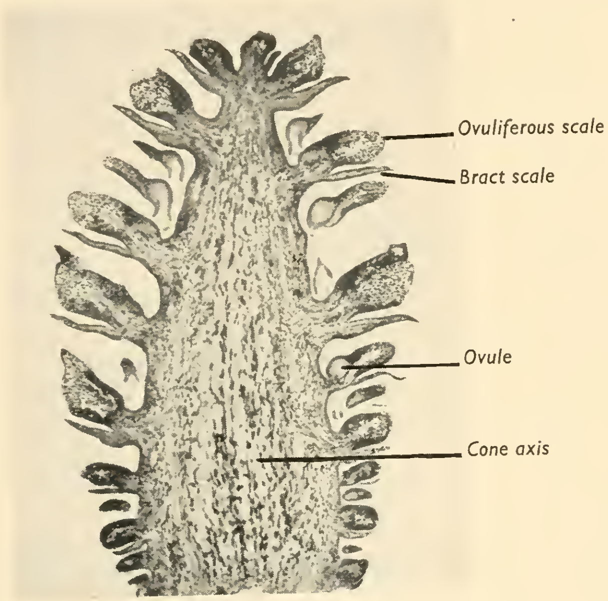

Fig. 677.—*Pinus sylvestris.* Longitudinal section of a young female cone at the pollination stage early in its first year. Note that the scales are well separated, thus admitting the microspores.

The classical theory is that of Alexander Braun (1853), who explained it as equivalent to the two leaves of a leaf spur, each bearing an ovule on its ventral (abaxial) surface, which have become united by their upper (anterior) margins. This would bring the ventral surfaces uppermost, as shown in the diagram (Fig. 678), which illustrates the supposed course of evolution. The theory finds support in the inverted position of the vascular bundles of the scale (xylems downwards) and in the development of the " double leaf " in the Cupressinean genus *Sciadopitys*, in which the suggested fusion actually occurs during the development of each leaf. How much importance should be attached to the vascular structure is doubtful, as similar inverted bundles occur in the cone scales of other Gymnosperms in which foliar spurs are unknown.

Variations of this theory are numerous. For example, Van Tieghem held that only one leaf of the axillary shoot was involved, namely the one which stood uppermost, opposite the bract. Zimmermann, on the other hand, concluded that the axillary shoot which has become the ovuliferous scale was entirely sporangiferous, and has been reduced from a multiovulate condition to the present condition with two ovules only.

The principal opposing theories have been :—

1. Sachs and Eichler. The ovuliferous scale is an outgrowth of the bract scale, comparable to a ligule or placenta.
2. Kubart and Bessey. The ovuliferous scale is a combined outgrowth of the ovules themselves, and might be called an aril or an enlargement of the chalaza of the ovules.
3. Delpino. The ovuliferous scale is formed from two lateral lobes of the bract scale which have been turned inwards and fused together.
4. Hirmer. The ovuliferous scale and the bract scale are both parts of one structure, which has forked vertically in the same way as the sporophylls in *Cheirostrobus* and other Sphenophyllales may have forked.

The extensive researches of Florin on the fossil Conifers may be regarded as giving decisive evidence in favour of the compound theory of the cone, which regards it as an inflorescence and the ovuliferous scales as short shoots.

The genus *Pseudovoltzia* (Permian) showed bract scales subtending an axial structure consisting of two anatropous ovules on long stalks, above which are five sterile bracteoles or scales. Fusion of the latter has produced the spur which is the ovuliferous scale, to which the stalks of the two remaining ovules are adnate. Later, in higher Conifers such as the Cupressineae, a further fusion of the ovuliferous scale with the bract scale takes place, the cone scales thus becoming simple, not double, structures (Fig. 679) (see also Volume III).

It may be mentioned that there is evidence from the genus *Podocarpus* that the male cone was primitively compound. In some species of that genus it is still compound, with simple sessile cones arising in the axils of bracts

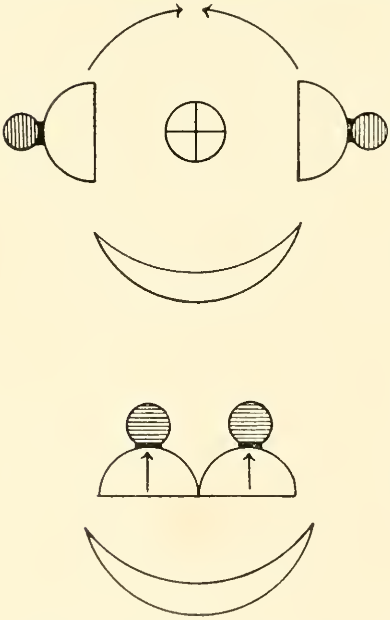

Fig. 678.—Diagram to illustrate Braun's theory of the origin of the ovuliferous scale. The ovules are shaded and the axis of the primitive axillary shoot is marked with a cross.

to form a compound strobilus. All stages of reduction from this condition to that of a simple cone may be found within the genus.

Whatever explanation is adopted it should apply to all Coniferales, as the female cones appear to be homologous throughout the order. The peculiarity of *Pinus* lies merely in the well-marked separation which exists between the two types of cone scale, but a duality of nature can be traced in the vascular anatomy of all cone scales, even those in which the two components seem to be most closely united.

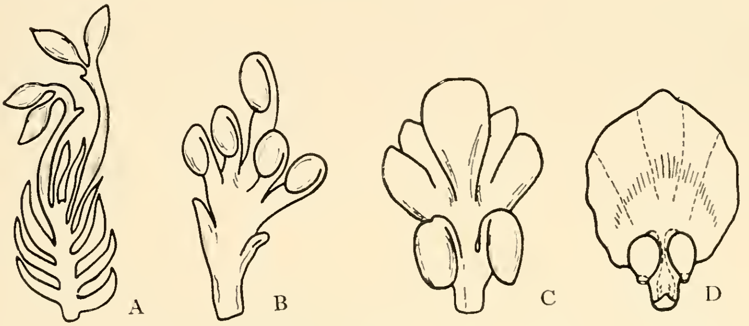

FIG. 679.—Fossil progenitors of the *Pinus* cone scale. A, *Cordaites pseudofluitans*, female strobilus. B, *Walchia germanica*, cone scale with five ovules and two sterile appendages. C, *Pseudovoltzia liebeana*, cone scale with two ovules and five sterile appendages. D, Modern Pine type, with two ovules and single sterile appendage, forming an ovuliferous scale. (*After Wilde.*)

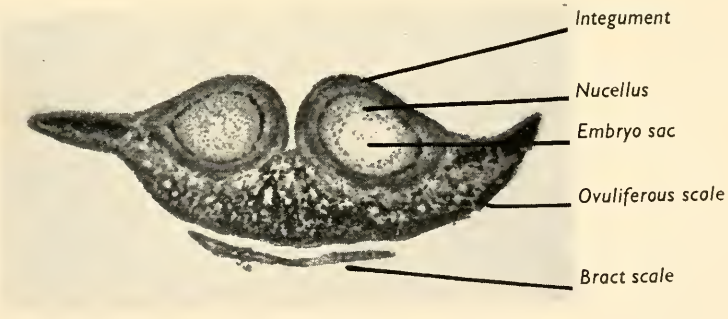

FIG. 680.—*Pinus sylvestris*. Vertical tangential section of a female cone scale passing through the two ovules and showing the position of the bract scale.

On the upper surface of the ovuliferous scale two **ovules** are produced side by side (Fig. 680). Each arises as a group of cells which forms a rounded hump of tissue termed the **nucellus**. This is rapidly surrounded by a two-lipped, covering layer termed the **integument**, which grows up around it, starting from the outer (abaxial) end of the nucellus and growing inwards towards the base of the cone scale (Fig. 681). At the inner end, which corresponds to the apex of the nucellus, a small uncovered aperture is left, called the **micropyle.** The integument is fused to the nucellus except for a short distance near the micropyle. Near the apex in the nucellus is a single large **archesporial cell.** It divides to form a single **tapetal cell** and a **megaspore mother cell.** The nucleus of the megaspore mother cell divides meiotically into four thus giving rise to a tetrad of four **megaspores.** Of these only one develops into a large cell which is termed, from analogy with the Angiosperms, the **embryo sac.** It is important to recognize that in *Pinus* only one megaspore mother cell is formed and that only one of its megaspores continues to develop. At the time of pollination only the megaspore has been formed and its development into the embryo sac is all subsequent to that event.

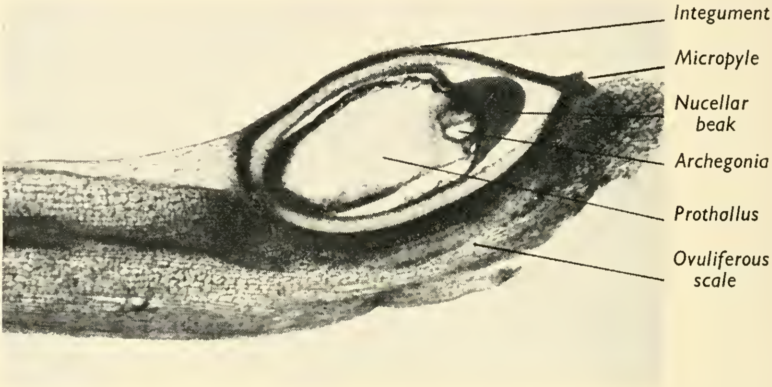

FIG. 681.—*Pinus sylvestris.* Longitudinal radial section of an ovuliferous scale passing through one of the ovules.

POLLINATION

The transference of the pollen grains to the ovule is effected by the wind. Towards the end of May the microspores are liberated in vast quantities, of which some small part falls on the scales of the female cone. The edges of the bract scales become inrolled, thus forcing the ovuliferous scales apart, which allows the pollen to gain access to the ovules. Prior to this the scales have been tightly closed around the axis of the cone, enclosing and protecting the rudiments of the reproductive organs, and after pollination they close again, remaining so until the seeds are ripe.

In addition to the opening of the scales the nucellus secretes a drop of a mucilaginous fluid in which the microspores become entangled. After pollination this drop of liquid dries up, drawing the microspores through the micropyle to the apex of the nucellus, where they are held by the dried mucilage in a position suitable for germination. This position is ensured by the air sacs which float the microspore in the pollination drop with the thin-walled side downwards. This side, from which the pollen tube develops, is thus brought into contact with the surface of the nucellus.

THE MALE GAMETOPHYTE.

Before the pollen is shed the first nuclear division has occurred, and immediately after pollination a second division of the nucleus of the tube cell produces a **second prothallial cell** on top of the first, equally flattened and evanescent (Fig. 682).

The remaining nucleus now divides a third time, cutting off a large, rounded cell on top of the degenerating prothallial cells. This is the **antheridial cell,** so called because it produces the male generative cells, though it forms nothing resembling an antheridium in structure. The nucleus which remains in the tube cell of the microspore apparently controls the germination of the spore and is called the **tube nucleus** (Fig. 683).

When the microspore has made contact with the tip of the nucellus the exo-intine breaks between the air sacs and the intine grows out to form the beginning of the **pollen tube,** into which the tube nucleus passes. The pollen tube penetrates into the nucellar tissue and grows slowly throughout the ensuing summer. Meanwhile the scales of the female cone thicken till the cone is once more completely closed, thus shutting in the developing pollen, which rests throughout the first winter.

The following April the pollen tube begins to grow again. The antheridial cell divides into two cells, one of which we may call the **body cell** and the other the **stalk cell.** The latter may represent the stalk of an ancestral antheridium, while the body cell is a vestige of the remainder of the antheridium. The stalk cell functions simply as a support for the body cell and develops no further. The body cell divides into two unequal cells with scanty cytoplasm and very large nuclei. If we were dealing with a fully organized antheridium we would say these were antherozoid mother cells, but they actually function as male gametes without developing into antherozoids, so it is perhaps simplest to call them the **male cells.**

THE FEMALE GAMETOPHYTE

During the period which succeeds pollination the female cone increases greatly in size, it turns green, and both the axis and the ovuliferous scales become very much enlarged. By the end of the first year it is about 4 to 5 cm. long (Fig. 684).

Meanwhile the development of the ovule continues. The megaspore enlarges and its nucleus divides some eleven times in succession, giving about two thousand nuclei, which are arranged in a layer of protoplasm around the periphery of the embryo sac, surrounding a large central vacuole. These are all " free " nuclei with, at first, no intervening walls. New walls then begin to appear, growing inwards from the megaspore or embryo sac wall, and these walls grow centripetally, like open tubes, drawing the cytoplasm with them, until they meet at what was previously the middle of the vacuole. The embryo

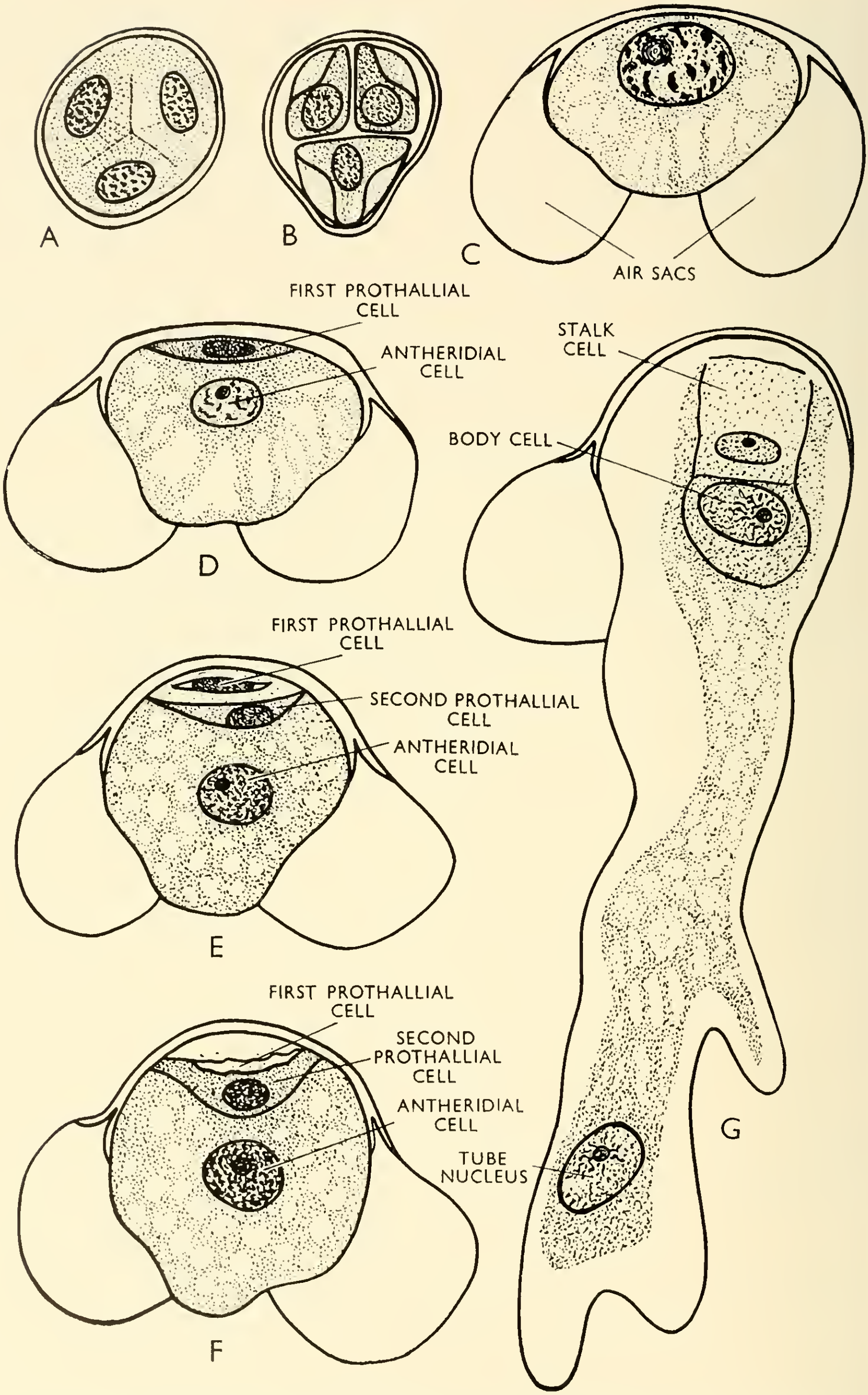

Fig. 682.—*Pinus sylvestris.* Development of the male gametophyte. A, Division of microspore mother cell. B, Completed tetrad of microspores with the mother cell. C, Mature microspore. D, Formation of first prothallial cell. E and F, Formation of second prothallial cell. G, Division of antheridial cell to form stalk cell, body cell and tube nucleus. Compare with Fig. 683. (*After Coulter and Chamberlain.*)

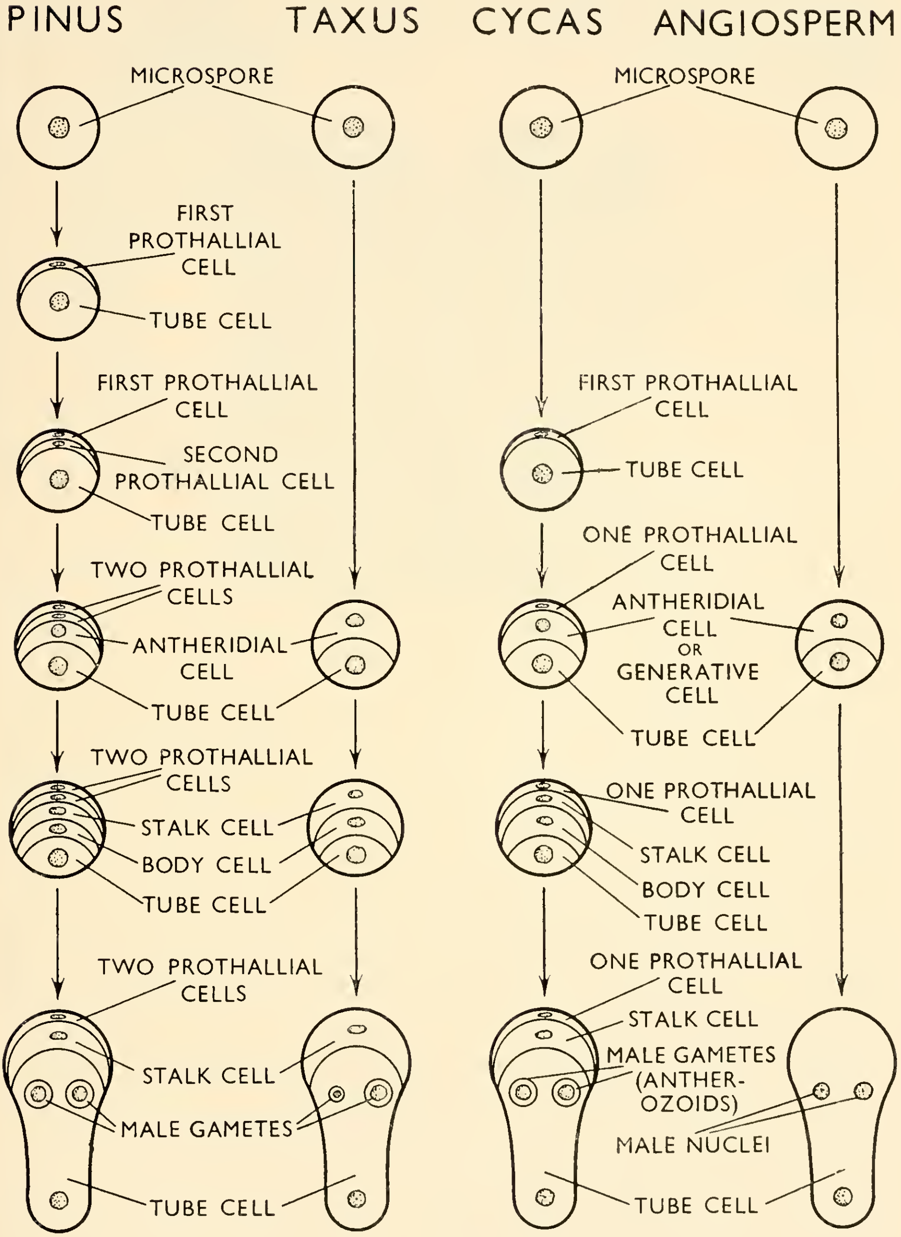

Fig. 683.—A comparison of the male gametophytes of *Pinus*, *Taxus*, *Cycas* and an Angiosperm showing varying degrees of reduction.

sac is thus cut into a number of radial spaces, each containing several nuclei, known as **alveoli** (Fig. 685). Cross walls then divide the alveoli into uninucleate cells, completing the formation of a tissue, sometimes called the **endosperm,** but which is really the **female prothallus,** contained in the megaspore (Fig. 686).

Fig. 684.—*Pinus sylvestris.* Female cone at the end of the first year.

The membrane round the embryo sac corresponds to the wall of the free megaspore in the Cryptogams. Although it is not so massive a structure as in *Selaginella* or *Isoetes*, it is better developed in *Pinus* and its allies than in most of the other Coniferales. As the prothallus grows the membrane thickens and finally differentiates into two layers, the inner one containing cellulose and the outer one completely suberized.

The megaspore is itself contained in the nucellus, which probably corresponds to a megasporangium. It should be noted that the whole of this development occurs without the megaspore being detached from the parent plant, so that the female prothallus is completely dependent on the sporophyte for its nutrition.

Around the prothallus the cells of the nucellus are transformed into a two-celled layer of nutritive tissue, called the **spongy layer,** which corresponds to a tapetum. At the micropylar end of the ovule, from one to five (usually three) archegonia are produced from superficial cells of the female prothallus. These archegonia are relatively simple structures, consisting of a large **venter** and a short **neck.** An **oosphere** and **ventral canal cell** are formed but there are no neck canal cells. At an early stage a layer of cells round each archegonium forms a **jacket layer** which supplies food to the oosphere. The adjacent cells of the prothallus grow faster than the neck cells so that the neck lies in a depression (Fig. 687).

The growth of the megaspore crushes the sides of the nucellus so that at

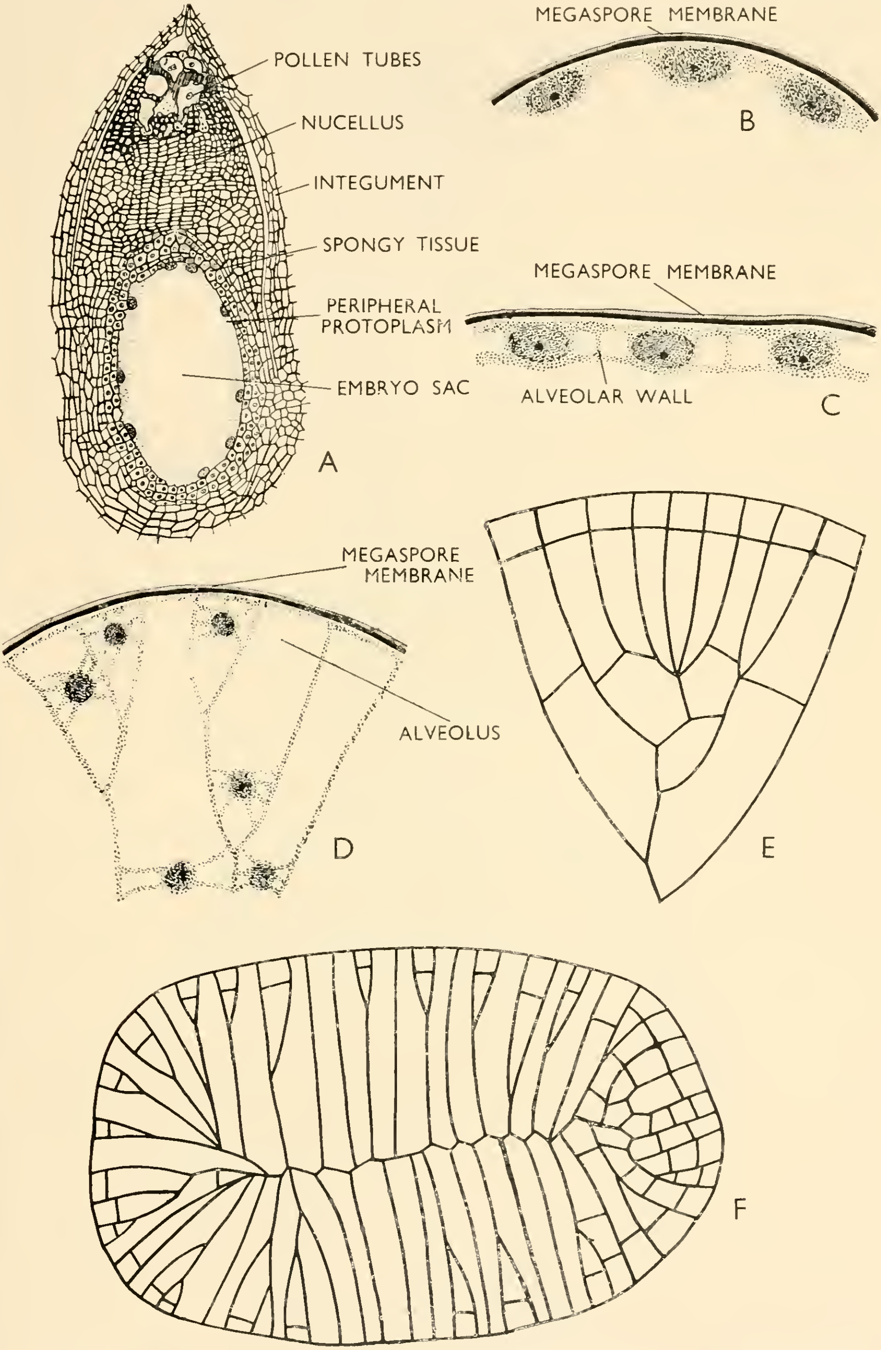

FIG. 685.—*Pinus sylvestris.* Development of the female prothallus. A, Longitudinal section through the nucellus of the ovule at the beginning of the second year. B, Margin of the embryo sac enlarged showing peripheral nuclei embedded in cytoplasm around a large central vacuole. C, As in B, showing commencement of alveolation. D, Alveoli extending into central vacuole. E, Segmentation of alveoli and deposition of cell walls. F, Completed alveolation and segmentation progressing to form the tissue of the female prothallus. (*After Sokolowa.*)

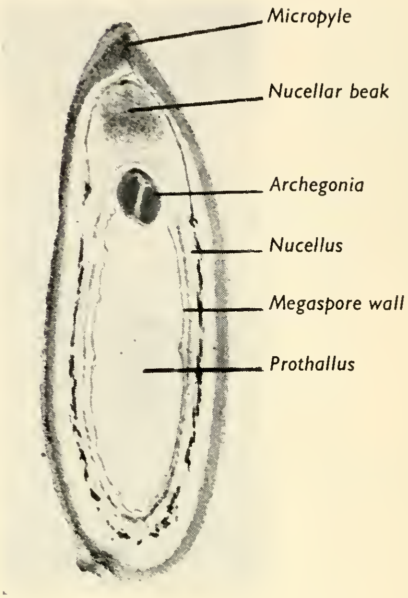

FIG. 686.—*Pinus sylvestris.* Longitudinal section of an ovule with archegonia at fertilization stage.

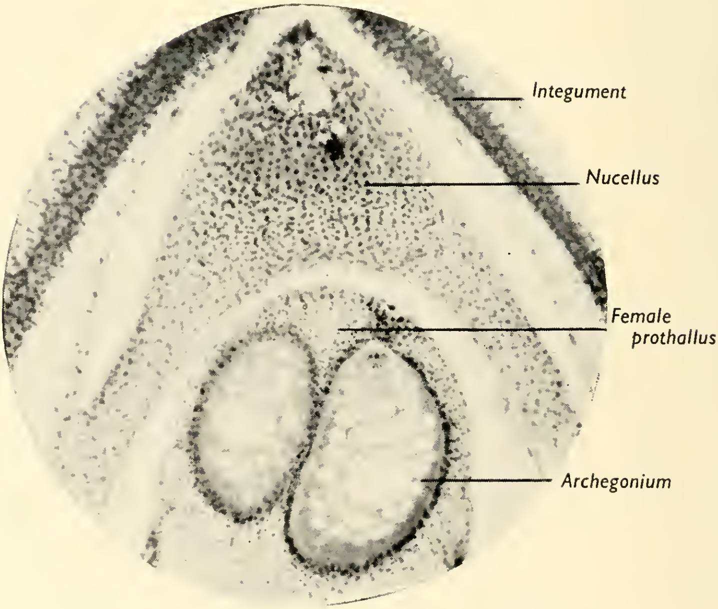

FIG. 687.—*Pinus sylvestris.* Enlarged view of the apical region of the ovule showing two archegonia.

maturity there is little of it left except the cone of tissue at the micropylar end, the cells of which are rich in starch. The tip of this cone becomes partially disorganized at the time of pollination.

The archegonia are essentially similar in structure to those of the Vascular Cryptogams, differing only in the larger venter and smaller and simpler neck, which is probably due to their enclosed position. The oosphere nucleus is central and very large. In the cytoplasm there are a number of peculiar vacuoles which appear to contain protein reserves and which stain like nuclei. They are sometimes called the **paranuclei** (Fig. 688).

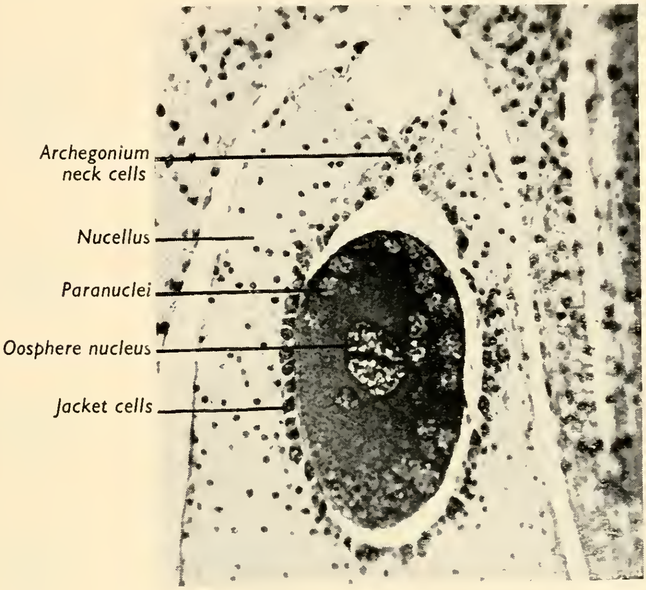

FIG. 688.—*Pinus sylvestris.* Longitudinal section through the apex of a female prothallus showing an archegonium with oosphere nucleus and paranuclei in the cytoplasm.

FERTILIZATION

During April of the second year the pollen tube becomes active again, and the male cells are formed from the antheridial body cell. The nuclei of the tube cell, and the stalk cell, with the male cells, all pass down to the apex of the pollen tube so that four nuclei are to be seen there.

The pollen tube makes its way down until it reaches the neck of one of the archegonia, often throwing out short branches. The end of the tube penetrates the neck, and the two nuclei with the complete male cells enter the oosphere, where all but one male cell disintegrate. The nucleus of this cell slips out of its cytoplasm and unites with the oosphere nucleus. The chromatin of the combined nucleus passes at once into mitosis and the two sets of chromosomes mingle on the equatorial plate. The process is usually completed in the last week of June.

More than one pollen tube may develop in association with a single ovule and more than one archegonium may be fertilized, but as there is only food material for one to come to maturity, the others die off after a short period of development.

EMBRYOGENY

The fertilized, diploid nucleus of the oospore divides twice and the four nuclei formed move to the bottom of the oospore (Fig. 689). There a third nuclear division takes place and the eight nuclei arrange themselves in two tiers of four, the lower four being cut off by walls. The upper, free nuclei are separated only by imperfect walls and they take no further part in the formation of the embryo. The lower cells divide once, so forming three tiers of four cells each, and a final division of the lowermost nuclei completes the

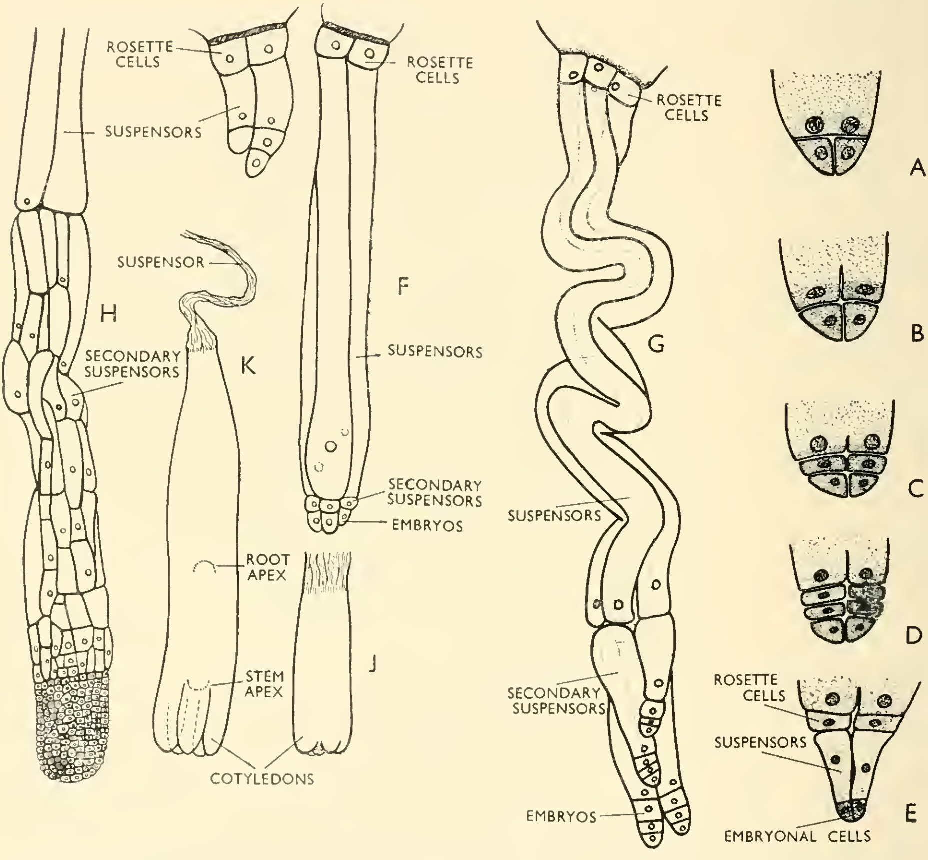

FIG. 689.—*Pinus sylvestris*. Development of the embryo. A to E, Successive division of the fertilized oosphere. F, Elongation of primary suspensors. G, Formation of secondary suspensors and separation of four embryonal groups. H, Development of a single embryo and multiplication of suspensor cells. J and K, Appearance of the cotyledons and differentiation of embryonic axis. (A *to* E *after Coulter and Chamberlain*, G *to* K *after Buchholz*.)

formation of four tiers. The lowest tier form the **embryonal cells,** the next above are the **suspensors,** and the third tier is called the **rosette tier.** As stated, the uppermost or fourth tier plays no further part. This symmetrical grouping of the pro-embryonal cells is characteristic of Coniferales as an order, though there are not always four tiers. The suspensors elongate very greatly and the embryonal cells are thrust down into the tissues of the female prothallus, which functions as a nourishing tissue (Fig. 690). It is a curious feature of embryogeny in *Pinus* that the four embryonal cells normally separate from each other and develop independently into four embryos, each of which develops secondary suspensor cells. The whole structure of each embryo, therefore, comes from one cell only. Such a condition, which is widely characteristic of the Coniferales, is termed **polyembryony,** or more strictly **cleavage polyembryony,** to distinguish it from the similar condition which may arise from the fertilization of more than one archegonium or by the development of embryos from the rosette cells. In the course of time, however, owing to a competition for food, only one of these embryos survives to come to maturity (Fig. 691).

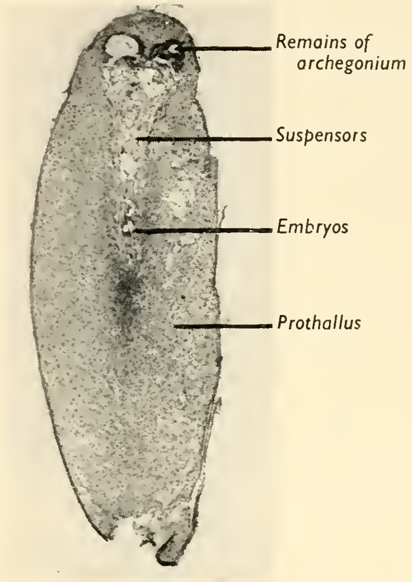

FIG. 690.—*Pinus sylvestris.* Longitudinal section of the female prothallus showing the penetration of the embryo into the prothallial tissue.

The developed embryo is straight, consisting of a short axis with the **radicle** towards the micropyle and the stem apex or **plumule** downwards. The plumule is surrounded by a group of about ten primary leaves or

cotyledons. The number may be reduced by fusions taking place, but it seems that polycotyledony is the primitive condition. In the early stages the embryo has a single apical cell, which recalls the embryonic development in Pteridophyta, but it is later replaced by a group of meristematic initials.

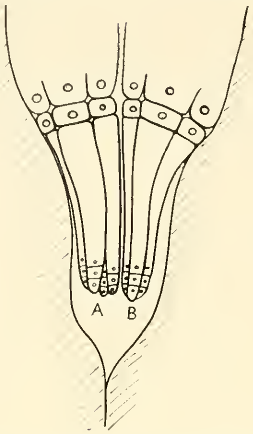

Fig. 691.—Diagram illustrating two conditions of polyembryony in the Abietineae. A, Cleavage polyembryony with four independent competing embryos. B, All four embryonal cells united to form one embryo. In the course of germinal competition between B and A, B will always survive. (*After Buchholz.*)

The central tissue of the female prothallus breaks down as its food materials are taken up by the embryo, leaving a space which is filled by the folds of the continually growing suspensor. When the embryo is mature the suspensor dries up and forms a thick cap over the root end of the embryo. The outer layers of the prothallus persist in the mature seed, surrounding the embryo with a nutritive tissue called the **endosperm.**

The integument of the ovule begins at an early stage to form a median layer of stone cells, and by the time the seed is mature the inner and outer layers of soft cells have disappeared, leaving only the stony layer, which forms the covering or **testa** of the seed. The seed therefore consists of only the stony testa, the endosperm and the embryo.

In the third year the female cone reaches maturity (Fig. 692). It is now a dry, brown, woody structure, bearing a pair of mature seeds on the surface of each ovuliferous scale. The seed has a thin **wing** which assists it in dissemination, this structure being derived from the surface of the ovuliferous scale. When the seeds are mature the cone scales spring apart explosively with cracking sounds, the separation being due to renewed growth in the cone axis. The seeds are liberated and are blown away by the wind as they fall from the cones.

GERMINATION

Pine seeds may germinate at once if they fall where they can absorb water, and in any case their dormant period is not long. The seed coat splits open and the radicle grows downwards into the soil while the plumule grows upwards towards the light (Fig. 693). The cotyledons become green, in fact this may occur before they are exposed to light. They carry up with them the remainder of the seed, and the tips of the cotyledons absorb what is left of the endosperm. The radicle passes downwards into the soil forming a primary tap root, while the developing plumule produces a shoot of unlimited growth upon which delicate needle leaves are produced in a spiral arrangement (Fig. 694). This condition, which may be regarded as primitive for the

FIG. 692.—*Pinus sylvestris.* Mature female cones in the third year, opening to liberate seeds.

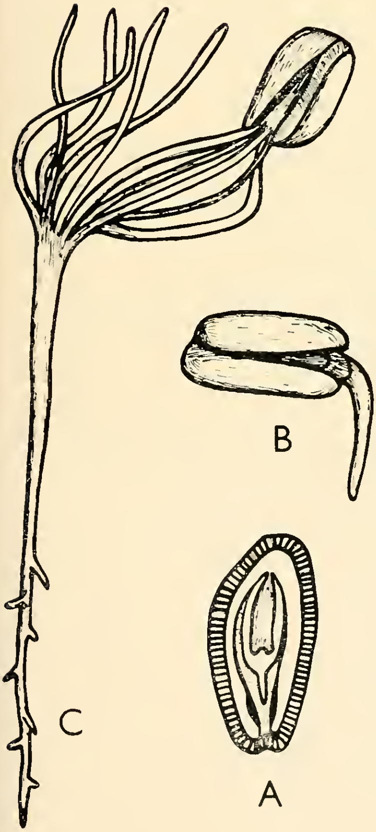

FIG. 693.—*Pinus sylvestris.* Germination. A, Longitudinal section of the seed showing a straight embryo surrounded by endosperm. B, Germination of seed. C, Liberation of numerous cotyledons from the seed and growth of the primary root. (*After Sachs.*)

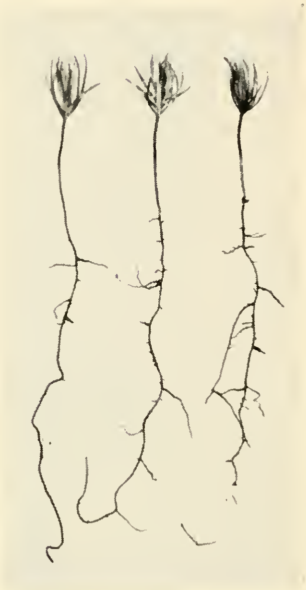

FIG. 694.—*Pinus sylvestris*. Young seedlings showing primary needle leaves.

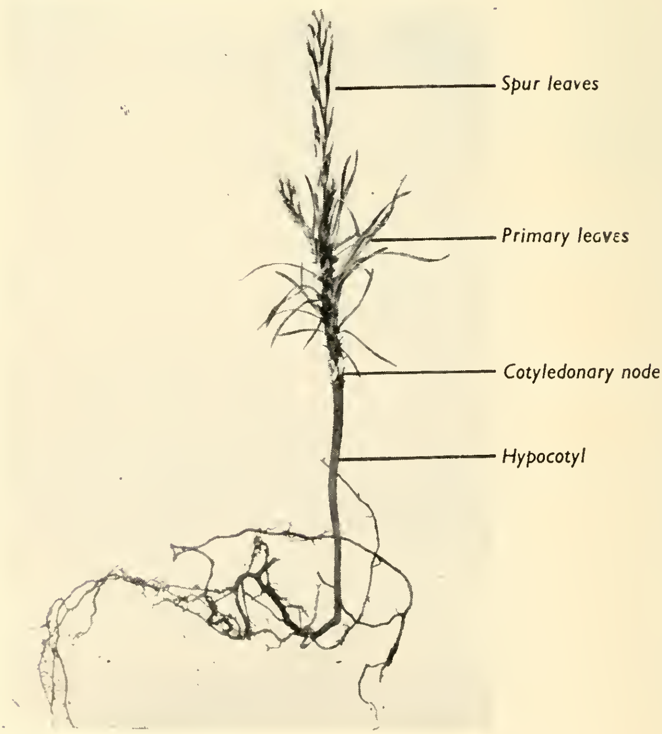

FIG. 695.—*Pinus sylvestris*. Older seedling showing replacement of primary leaves by leaves borne on spurs.

Pines, persists until the seedling is 3 or 4 in. high, when the first foliar spurs appear in the axils of the juvenile leaves. As the seedling continues to develop the later formed juvenile leaves become progressively smaller and pass over gradually into the scale leaves of the mature stem. This change over to the spur leaves probably represents a recapitulation of a similar change in the evolutionary history of the race (Fig. 695).

ALTERNATION OF GENERATIONS

We see then that in *Pinus* there is the same alternation of generations that we have met with in previous types. The chief points of interest being that in *Pinus* the gametophytes are still further reduced; they are entirely dependent upon the sporophyte for food and are retained within the spores. In fact the male gametophyte is represented by little more than the essential sex cells. In the female gametophyte an extensive tissue is formed, but its function is to nourish the developing embryo, and it obtains the food to do this, not by independent assimilation, but by transferring food from the sporophyte for this purpose. It functions, then, merely to transfer food and not as a supplier.

There is a still further reduction in the number of megaspores, which is now reduced to one, while there is a large production of microspores, only a very small proportion of which ever reach the female cone. Thus in *Pinus* there is a great wastage of fertilizing material, and we shall find that in the Angiosperms, methods have been found to reduce this wastage to a minimum.

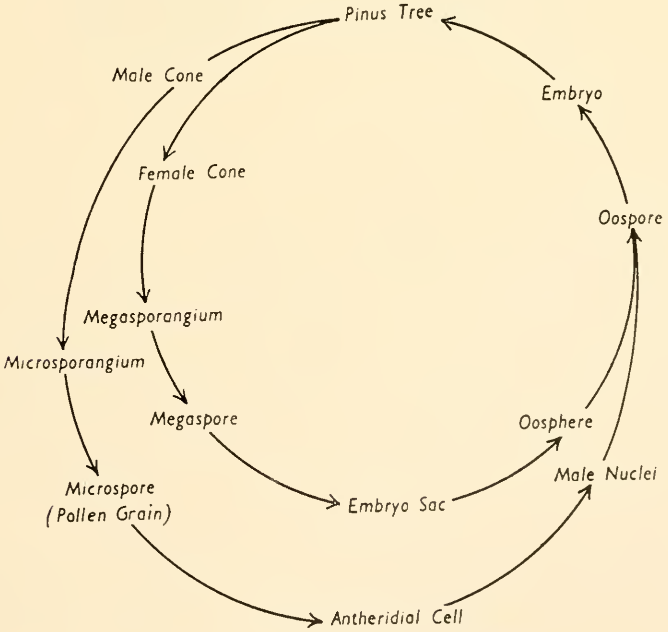

FIG. 696.—Life-cycle of *Pinus sylvestris*.

It is very important, however, to realize that the life-cycle of *Pinus* follows the same basic sequence as that of the previous types we have considered, and that the differences are those of modification rather than the occurrence of any fundamental change.

The life-cycle of *Pinus* may be graphically represented by Fig. 696.

Relationships and Phylogeny

The relationship of *Pinus* to other Gymnosperms has been a matter of much discussion. Opinion has been divided as to the most primitive Coniferous type, between the Abietineae, of which *Pinus* is a member, and the Araucariineae, which have simple cone scales and broad leaves. The tracheids in the latter group have several alternating rows of closely contiguous, hexagonal pits, while *Pinus* has either single rows or a few rows of circular, separated pits which are opposite, not alternate, to each other (Fig. 697). They also show thickened margins of pectose called " Rims of Sanio " after their discoverer (Fig. 698). The two types are readily distinguishable, even in the fossil state, and both can be traced back to the Palaeozoic. The Araucarian type is certainly nearer to that of the Cordaitales, but the value of this evidence is doubtful, for a good deal of variation occurs. Jeffrey, on the other hand, claims that the transfusion tissue in the *Pinus* leaf is directly related to that in the leaf of *Cordaites*, though the needles of the Pine are plainly reduced structures and borne on reduced shoots, while the flat leaves of *Araucaria* are superficially more akin to those of Cordaitean shoots.

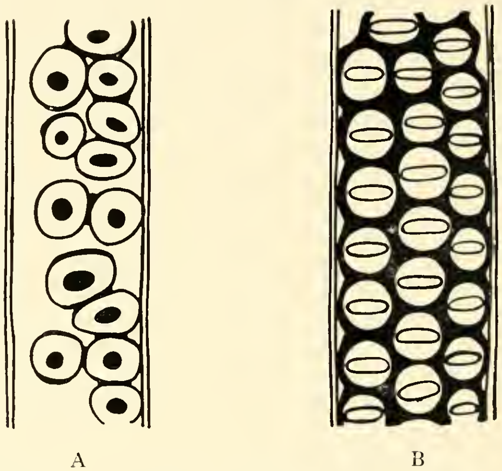

Fig. 697.—Comparison of the type of tracheidal pitting in A, Abietineae. B, Araucariineae. (*After Thompson.*)

A double leaf trace is characteristic of the Palaeozoic Gymnosperms. It is also found in *Araucaria* and to a lesser degree in *Pinus*, where it may be secondary in origin, as it is not present in the cotyledons as it is in *Araucaria*.

The cotyledonary bundles in some species of *Pinus* are mesarch, that is to say, some centripetal xylem is present, which is characteristic of the extinct Gymnosperms. On the other hand this is absent in the Araucarians.

Another primitive character in *Araucaria* is the persistence of the leaf traces, even in the wood of old trees, while the elaborate resin-canal system of *Pinus* might be regarded as an advanced type of structure.

The confusing picture presented by such apparently contradictory evidence is a salutary warning against too great a reliance on anatomical features in questions of evolutionary history. It is absurd to assume, as has sometimes been done, that certain supposedly " primitive " features of structure must necessarily stamp the whole plant as primitive, for the juxtaposition of old and new characters is by no means uncommon and might indeed be expected from the degree of independence in development exhibited by plant structures.

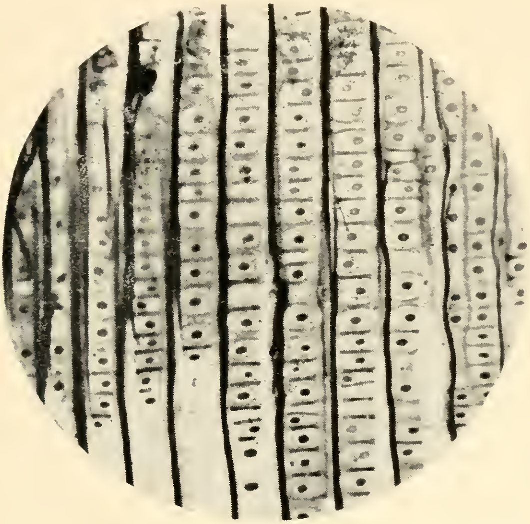

Fig. 698.—*Pinus sylvestris.* Longitudinal radial section of secondary wood stained to show Rims of Sanio.

Whichever may be the oldest group of the living Coniferales the connection of the order as a whole with the Cordaitales and through them with the Pteridosperms is scarcely open to doubt, and we must look to the fossil record for the final solution of the obscurities remaining in the problem.

Taxales

The order Taxales, as we shall here regard it, consists of a single family, Taxaceae, containing three genera, *Taxus*, *Cephalotaxus* and *Torreya*. The Podocarpineae, which were formerly included in this group, are now recognized to be more nearly related to the Araucariineae and included in the Coniferales.

Taxus has a single species which is distributed over Europe and the Mediterranean region, as far east as Persia. Its northern limit is about 61° N. It also occurs in eastern Asia and in North America.

Torreya is limited to one species in Japan, one in California and one in Florida. It is sometimes placed in a separate family.

Cephalotaxus has five species in south-east Asia and one in southern Japan (Fig. 699).

They are separated from the Coniferales by the absence of a female cone, the ovules being borne singly at the apices of very short shoots and on different plants from the males. In *Cephalotaxus* the ovuliferous shoot has been reduced to the vanishing point, so that the ovule appears to stand in the axil of a bract.

The nucellus is completely free from the integument in its early stages, but during development after pollination there is a considerable amount of intercalary growth at the base or chalaza of the ovule, so that eventually the free portion of the nucellus represents only a small apical part of the whole. Normally only a single seed matures from each female inflorescence and this is surrounded by a fleshy outer covering, the so-called **aril,** which may be free from the integument or united to it, and is considered by some to be equivalent to a second integument.

The pollen grains are smooth and wingless. No prothallial cells are formed in the male gametophyte and in *Taxus* and *Torreya* the cytoplasm of the male cell enters the oosphere with the fertilizing male nucleus and envelops the fusion nucleus. In the archegonium there is no evidence of any ventral canal cell being formed, though a very ephemeral ventral canal nucleus may be produced, which is evidently on the way to complete elimination. This is apparently also the case with the megaspore membrane, which is scarcely developed at all and never thickens as it does in the Abietineae.

Torreya has features in the seed which are highly peculiar. There is a vascular plate at the base of the nucellus which sends branches into the nucellus itself and these connect with a peculiar mucilaginous layer surrounding the nucellus, which, it has been suggested, may represent the vascular mantle that encloses the nucellus in some Palaeozoic Pteridosperm seeds. Nucellar vascular tissue is found in the relatively primitive Cycadales, but it has disappeared from the Coniferales. The basal growth of the ovule carries the nucellar bundles upwards, so that in the mature seed they are found entering the nucellus at the bottom of the apical, free part, through openings or foramina in the stony wall of the testa. *Torreya* also has a very vigorously growing endosperm, which encroaches on the surrounding tissues in an irregular fashion, producing an extremely complicated outline. This is also found in a few Angiosperms and is called **ruminate endosperm.**

There are certain points of vegetative anatomy which distinguish the group. One is the presence of centripetal xylem in the cotyledonary bundles, occasionally also in the stem axis and, notably, in the aril of *Cephalotaxus,*

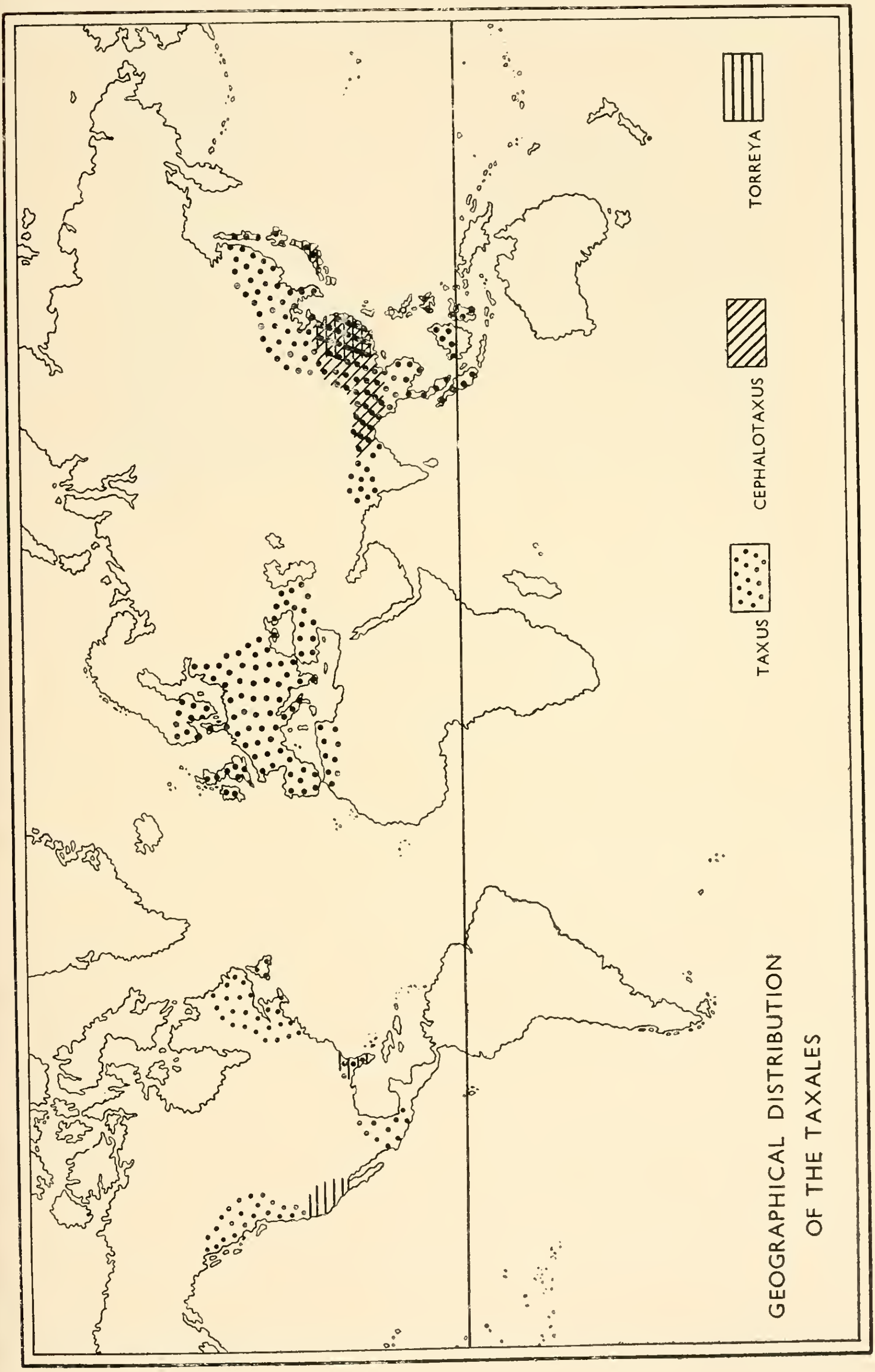

Fig. 699.—Geographical distribution of the Taxales.

where it is quite extensive and has a separate protoxylem, distinct from that of the centrifugal xylem. The latter feature recalls the similar structure in the sporophyll of *Cycas* and may be perhaps looked upon as a link with the Cycads.

On the other hand the leaf traces are consistently single, not double, which, in the light of comparison can only be regarded as an advanced character and remote from any suggestion of Cycadean affinities.

Resin canals of the *Pinus* type are altogether absent from this group. Indeed *Taxus* has no resin glands of any kind, though in the other two genera elongated resin sacs occur, especially in the leaves and the flower parts.

The characters of the Taxales make up a rather perplexing whole. They certainly stand well apart from the Coniferales, their nearest living link being possibly to *Ginkgo*. Geologically their remains do not go back beyond the Cretaceous period, so that it is impossible to connect them directly with any Palaeozoic group, but their morphological peculiarities, their small numbers and their discontinuous geographical distribution all seem to indicate that they are a group which has had an ancient history and is now decadent.

The possibilities are in favour of the derivation of Taxales from the same ancestral stock as the Coniferales, but they must have separated from the latter at an early date and have preserved some features of the ancestral stock, presumably the Cordaitales, which have since been lost by the Conifers.

Taxus baccata (The Yew)

There is only one species of *Taxus*, though there are a number of subspecies, some of which range farther than the type, several occurring in North America and one or two in Japan.

It is a slow-growing, evergreen tree, seldom reaching a height of more than 30 ft. (Fig. 700), although specimens estimated to be 3,000 years old are known, the oldest of which, a mere hollow shell, stands in the churchyard of Fortingal in Perthshire, Scotland. Molisch has, however, shown good reason for believing that these estimates of age are exaggerated, the enormously thick trunks having probably originated by the fusion of several small ones.

No foliar spurs are formed, and the branches grow horizontally and form a very dense canopy. The leaves are 2 to 3 cm. long, narrow and obtuse, and are borne spirally, but are twisted at their bases so that they lie in two rows along the horizontal branches. In certain varieties with upright branching the leaves are disposed all round the shoots, so that the two-ranked arrangement in the normal form is apparently a response to the horizontal growth of the branches.

Anatomically *Taxus* conforms to the general type of *Pinus*, with certain minor differences. There are no resin glands of any kind and the tracheids of the secondary wood show a spiral marking, in addition to bordered pits in a single series, as in *Pinus*. A single vascular bundle supplies the leaf, forming a midrib, flanked on each side by transfusion tissue (Fig. 701).

FIG. 700.—*Taxus baccata.* A full-grown tree in a country churchyard.

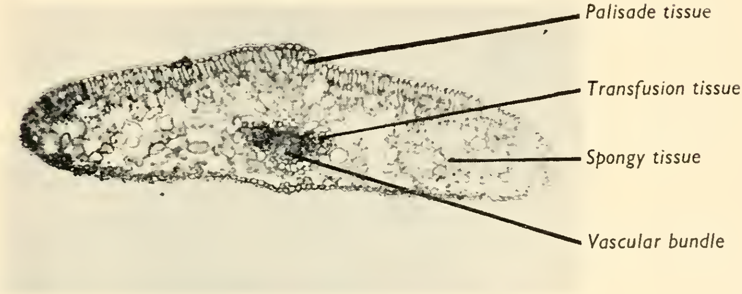

FIG. 701.—*Taxus baccata.* Transverse section of the leaf.

REPRODUCTION

The Yew is dioecious like other members of the order, but apart from the reproductive organs there is no apparent difference between trees of the two sexes.

THE MALE CONE

The male strobili are borne in the axils of the leaves on shoots of the preceding year and usually appear in February (Fig. 702). Each consists of a very short axis bearing at its base about a dozen bract-scales, spirally inserted, increasing in size upwards. The top of the axis bears a cluster of male sporophylls, so closely inserted as to appear umbellate (Fig. 703). There is no vegetative apex. Each sporophyll ends in a peltate shield, like the head of an umbrella, beneath which are six to eight oval pollen sacs, united to the stalk of the sporophyll and to one another. These open by the breakdown of all that part of the wall nearest the axis and the curling back of the upper part, with the peltate shield, as if the umbrella had turned inside out. Thus the pollen is easily dispersed by the wind. It is caught by a **pollination-drop** of liquid at the micropyle of the ovule.

FIG. 702.—*Taxus baccata.* Shoot bearing male strobili.

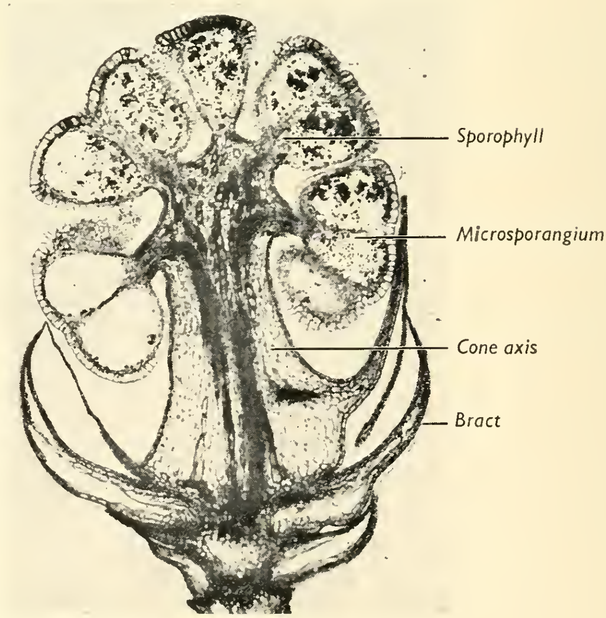

FIG. 703.—*Taxus baccata.* Longitudinal section of a male strobilus.

The Male Gametophyte

Development of the male gametophyte usually begins at pollination, that is, about the middle of March. The sequence of events is not quite certain but appears to begin with the division of the pollen grain into an antheridial cell and a tube cell. The antheridial cell then divides into a stalk cell and a body cell. The latter divides into two unequal male cells. All four nuclei pass into the archegonium, where the larger of the two male nuclei unites with the oosphere nucleus and the other three abort.

The Ovule

The ovules appear at the same time and in the same axillary position as the male cones, but upon different trees (Fig. 704). As in the male there is a short axis, called the **primary axis,** which bears a closely imbricated succession of sterile scales on its lower portion. From the axil of the uppermost of these involucral scales arises the fertile shoot, called the **secondary axis.** This bears three, crossed pairs of minute scales, the lowest pair standing transversely to the subtending bract. The ovule is apparently terminal on

FIG. 704.—*Taxus baccata.* Shoot bearing ovules surrounded by cupules.

this secondary axis. In the axil of the penultimate bract (*i.e.*, the eighth, counting downwards from the apex of the secondary shoot) there is a bud which was formerly regarded as the apex of the primary axis, but which is now known to be an arrested secondary shoot which sometimes develops and produces a second ovule. The vegetative apex of the primary shoot seems to be suppressed, but occasionally it proliferates after a seed has been formed and again produces a secondary axis and an ovule in the following year. The position of the first ovule is then marked by a lateral scar.

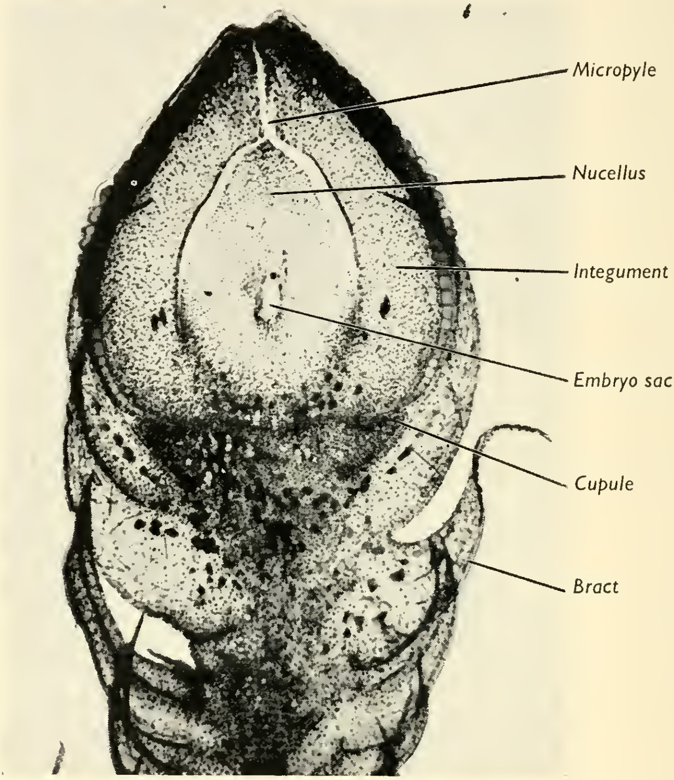

FIG. 705.—*Taxus baccata.* Longitudinal section of the ovule and ovuliferous branch.

The ovule is somewhat flattened, transversely to the uppermost pair of bracts, and the ripened seed is therefore oval in section, with two lateral ribs. Three and four ribbed seeds also occur as exceptions. There is a single, thick integument, which forms a rather long micropylar canal above the nucellus (Fig. 705). Two vascular bundles supply this integument, running along the lateral ribs. These bundles arise by the fusion of two pairs in the stalk of the ovule, one pair branching from the traces of the penultimate pair of bracts and the other pair from those of the uppermost pair of bracts.

Immediately below the integument there arises a ring-like swelling which slowly grows and surrounds the whole ovule. This is commonly called the aril, but it is a misnomer, for the structure is not the same as those outgrowths of the seed coat which bear this name among the Angiosperms. It has been more justly compared with the epimatium, secondary covering of the ovule in the Podocarpineae. Some consider it to be an outer integument, but in the absence of any decision as to its true nature we shall here refer to it as the **cupule**. Although it starts as a ring, its upward growth is slightly two-lipped and it receives two minute and almost abortive strands of scattered tracheids, arising as branches from the base of the integumentary strands. It may therefore be derived from two fused bract scales, just as the integument itself may be similarly derived. One may recall in this connection the two-lipped formation of the integument in *Pinus*.

The integument later develops a very hard, stony layer outside the vascular bundles, and this is covered externally by three layers of cells forming a thin brown skin which is soon detached, leaving the stony layer as the exterior coat of the ripe seed.

During the lignification of the stony layer a tube-like sheath of cells, with thick yellow cuticle, develops around the micropyle, the resistance of which prevents the micropyle from being closed by the growth of the integument.

The vascular bundles of the integument penetrate this stony layer at the base through two pores or **foramina.** These may be compared with the lateral foramina in the seed of *Torreya* (see p. 696), which also admit vascular bundles from outside, but lie near the apex of the seed. Sahni has suggested that this condition in *Torreya* may have been derived from the *Taxus* condition by the expansion of the seed base. This corroborates Oliver's theory that the whole of the lower part of the seed in *Torreya* is a secondary development, added, in the course of evolution, from seeds of the Cordaitalean type, in which the bundles penetrate the stony integument at the base (Fig. 706).

During the development of the seed in *Taxus* there is apparently a considerable amount of intercalary growth at the base. While the whole of the nucellus is free from the integument in the young state, the free portion is reduced to a small apical zone in the ripened ovule, the lower portion between the base of the seed and the limits of the free nucellus having developed secondarily. It is interesting to note that the two integumental bundles are bent into a knee-like flexure just above the point at which they penetrate the stony integument and that they are thickened at this bend. Sahni considers that this marks the place at which the vanished nucellar strands were formerly given off, such as existed in the Cordaitalean seeds. The nucellar traces in *Torreya* are probably the only relic of this interior system now surviving in Taxales or Coniferales, which may have been important only when fertilization by free antherozoids was the rule, for abundant secretion of moisture by the nucellus would then be essential.

The archesporium may be recognisable in the young ovule before the integument is mature, but the development of the female gametophyte is not completed until the following spring.

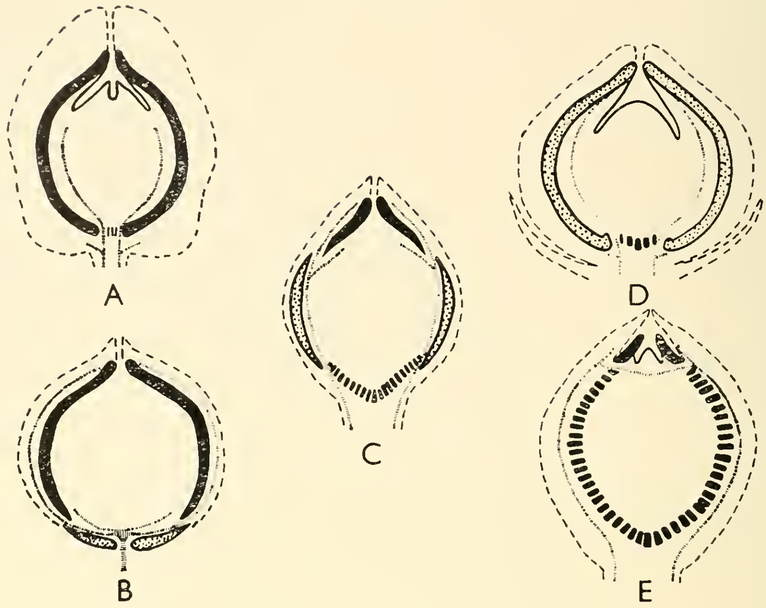

FIG. 706.—Comparison of the structure of the seed in *Taxus* and some related forms. A, *Ginkgo*. B, *Taxospermum* (fossil). C, Pre-*Torreya* stage (hypothetical). D, *Taxus*. E, *Torreya*. Vascular bundles transversely hatched ; external outline of seed, broken lines ; inner stony integument, black ; outer stony integument, stippled ; intercalated stony integument, interrupted black. The diagrams illustrate varying development of the inner and outer vascular systems in the integument and the intercalated growth at the base of the seed which results, in *Torreya*, in the displacement of the basal foramina to a position near the apex. (*After Sahni.*)

There may be one or several archesporial cells placed hypodermally at the apex of the nucellus (Fig. 707). They divide periclinally producing an upper cell, *i.e.*, the primary wall cell, and a lower cell, *i.e.*, the primary sporogenous cell. The primary wall cell divides repeatedly in a periclinal direction, building up a row of cells between the primary sporogenous cell and the surface of the nucellus. In this development other cells of the nucellus also take part.

The primary sporogenous cell or cells also divide repeatedly and produce a compact mass of sporogenous tissue. One or more of these cells elongate and become megaspore mother cells. Each megaspore mother cell divides transversely into four cells, of which one, usually the lowermost, functions as a megaspore and develops into an embryo sac. The others presumably abort, though cases of double embryo sacs in mature ovules have been recorded.

Pollination takes place about the middle of March, while the nucellus is still an homogeneous tissue. The pollen tube grows into the apex of the nucellus, where it destroys a number of cells and creates a hollow. At this stage it rests until the archegonia have been formed.

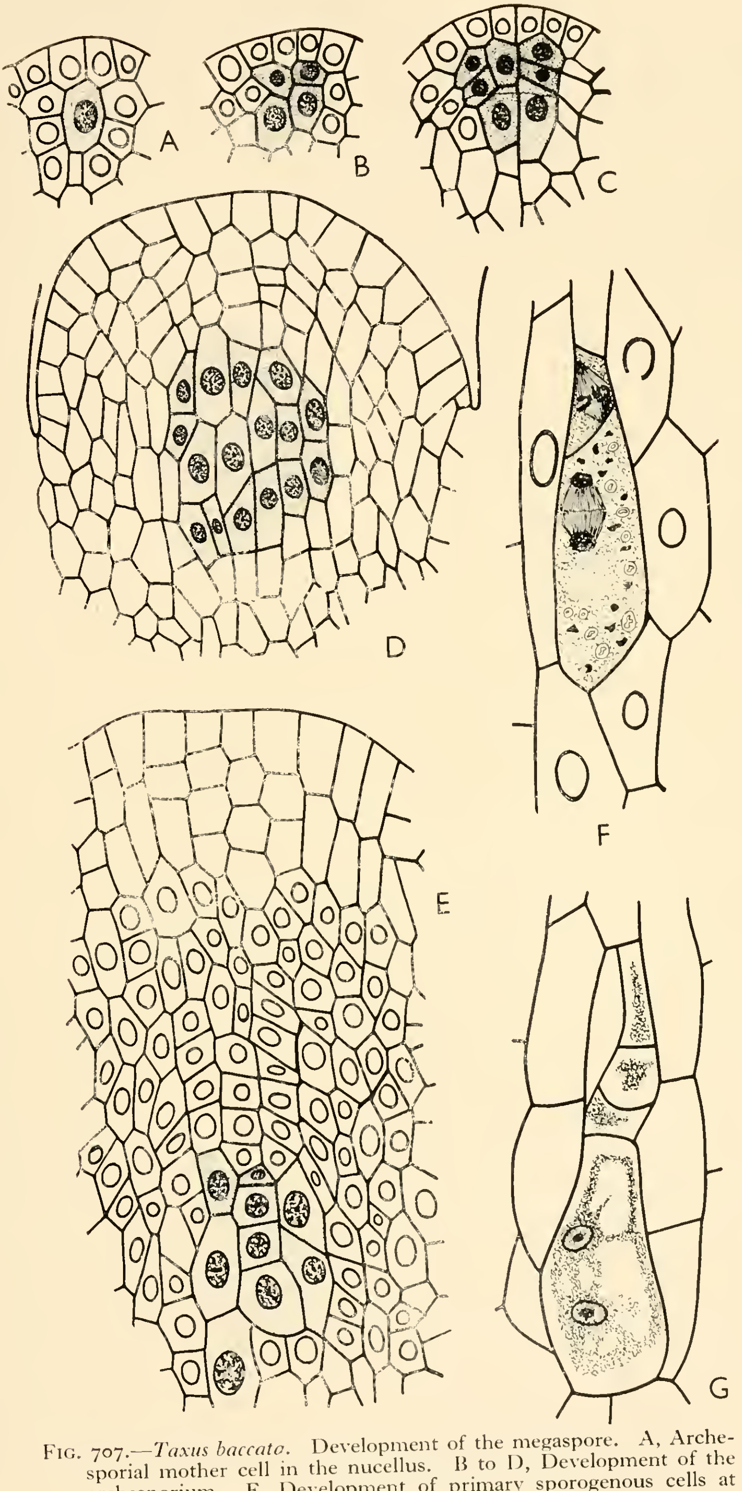

Fig. 707.—*Taxus baccata.* Development of the megaspore. A, Archesporial mother cell in the nucellus. B to D, Development of the archesporium. E, Development of primary sporogenous cells at the lower ends of rows of archesporial cells. F, Meiotic division of a sporogenous cell which functions as a megaspore mother cell. G, Row of four megaspores, upper three abortive, lowest developing into embryo sac. (*After Dupler.*)

THE FEMALE GAMETOPHYTE.

The nucleus of the megaspore divides to form 256 free nuclei, arranged round the periphery of the rapidly enlarging cell. The formation of the prothallial tissue follows by centripetal alveolation, very much as in *Pinus*, but the completed prothallus has a longitudinal strand of elongated cells, suggesting a conducting function, which is peculiar to *Taxus*. Although the prothallus cells are primarily uninucleate there is a multiplication of their nuclei during July so that eventually each cell may contain up to sixteen nuclei, except in the central strand of cells where there are rarely more than three or four. Finally the nuclei in each cell degenerate and fuse, first into three or four masses and finally into one large irregular mass.

The number of archegonia varies, usually between five and eight. They originate from cells two or three deep from the upper surface of the prothallus and may be united in a close group or may be variously distributed in the tissues. Often the prothallus tissue proliferates around the archegonia, rising beyond them so that they are left at the bottom of deep pits. Each archegonium is very simple. There are only four neck cells and no ventral canal cell has been recorded.

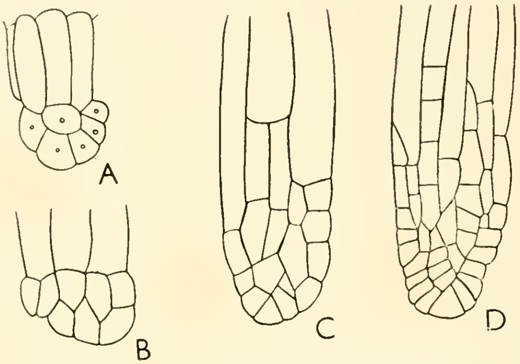

FIG. 708.—*Taxus baccata.* A and B, Development of the embryo showing elongated suspensor cells and embryonal group. C and D show the organization of a pyramidal apical cell. (*After Strasburger.*)

Several archegonia may be fertilized, but only one embryo normally develops to completion. The first stage is free nuclear division in the oospore, up to thirty-two nuclei being formed before they migrate to the base of the oospore, when wall formation divides them into separate cells, which are arranged in three layers. The lowest layer forms the embryo and the middle layer the suspensors, very much as in *Pinus* (Fig. 708). The mature embryo is straight and has two cotyledons. It consumes all the endosperm (prothallus) during its maturation.

The seedling has two linear cotyledons which remain until the third year. They are somewhat larger than the foliage leaves which follow them, but are otherwise similar and have a single vascular bundle. The primary root is diarch and lateral roots soon begin to appear.

CHAPTER XVIII

THE GYMNOSPERMAE: CYCADALES, GINKGOALES AND GNETALES

Cycadales

The order Cycadales includes one family, the Cycadaceae, which is a small group of genera distributed over the warmer parts of the globe, though nowhere very abundant. They are of small account in the vegetation of the present day, but they are of great botanical interest as the remnant of a group which reached its zenith in the Cretaceous period and which can be traced back throughout the Mesozoic era. Many features in their organization are more primitive than anything found in the Coniferales, and they show evidence of a fairly close connection with the great Palaeozoic group of the Pteridospermae, from which most of the modern Flowering Plants are probably derived.

Morphologically they occupy an intermediate position between the Pteridosperms and the Angiosperms, and although none of the living Cycads can be considered to be a direct ancestor of the Angiosperms, there is a strong probability that the latter group sprang from an earlier Cycadean stock.

The nine living genera are all of somewhat similar habit, having usually short, thick stems crowned by a cluster of very large pinnate leaves, so that they resemble in aspect the Tree Ferns or some Palms. Their growth is very slow and branching is rare.

The principal difference between the Cycads and the Pteridosperms is that in the Cycads the sporophylls are organized into distinct strobili or cones, which are borne at the apex of the stem or, in some cases, laterally, but near the apex. They are very much larger than the cones of the Pines, being sometimes as much as 3 ft. long and 9 in. thick. Unlike the Conifers, the Cycads are all dioecious.

The discontinuous geographical distribution and the small areas occupied by most of the individual genera are characteristic of old and decadent groups. In the middle part of the Mesozoic era the Cycads seem to have been so much more abundant and widespread than at the present day that this geological period has sometimes been called the "Age of Cycads," but this is not strictly correct, since the dominant plants of that period were the similar but hermaphrodite Bennettitales with which their fossil remains were formerly confused.

The following are the leading characteristics of the living genera:

Cycas. The most primitive genus, with sporophylls of primitive leaf-like form, which suggest a close connection with the Pteridospermae. The genus occurs in Africa, Australia and East Asia.

Microcycas. This genus has the most primitive gametophytes in the order. The pollen grains form sixteen or more antherozoids, and the female prothallus produces as many as two hundred archegonia. There is only one species, *M. calocoma*, confined to Cuba.

Zamia. Comparatively small plants with the stems usually underground and tuberous. They occur in tropical America from Florida to Chile.

Macrozamia. Large and not infrequently branched. The cones are the largest in the order and are sometimes truly lateral. The heavy seeds are forcibly ejected to a distance of several yards. *M. moorei*, in Queensland, is poisonous to stock and is eradicated by injecting with arsenic. The genus is confined to Australia.

FIG. 709.—*Encephalartos horridus* photographed in Kew Gardens.

Ceratozamia. The ovulate sporophylls have two spines which give the plant its name. The genus occurs in southern Mexico.

Dioon. Comparatively dwarf plants. The ovulate sporophylls have long overlapping points. The genus occurs in southern Mexico.

Stangeria. The only genus with network venation in the leaves, which are remarkably fern-like. The genus occurs in South-east Africa.

Encephalartos. The ovulate sporophylls are shield-shaped, somewhat like those of *Zamia*, and do not overlap as in *Dioon.* The name arises from the fact that one species yields an edible pith from the crown of the stem. The genus occurs in South Africa (Fig. 709).

Bowenia. The leaves are bipinnate and spreading. The genus occurs in Queensland (Fig. 710).

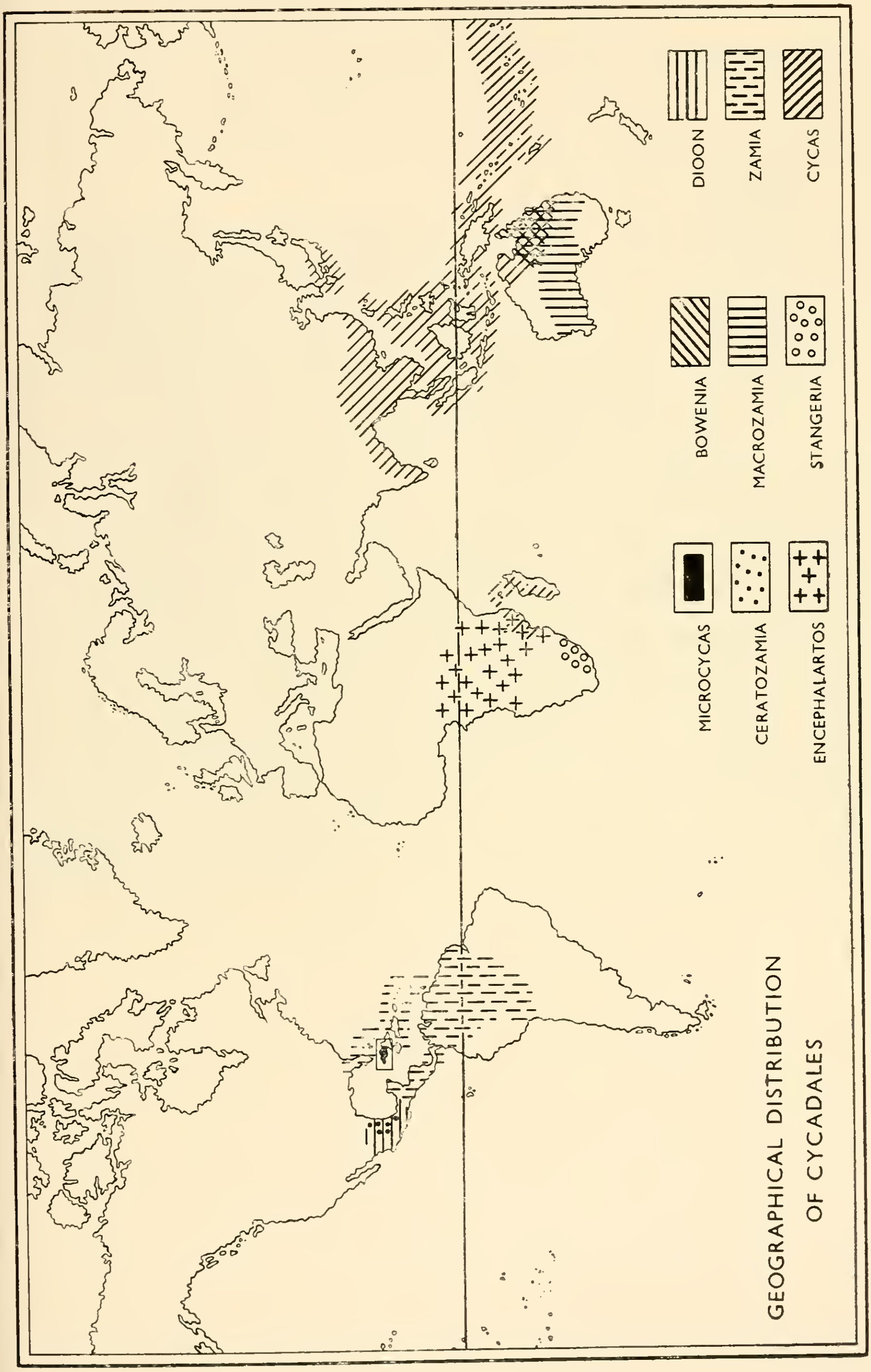

Fig. 710.—Geographical distribution of the Cycadales.

Cycas revoluta (The Sago Palm)

This interesting species has been called " a living fossil " on account of its primitive characteristics. It is native to southern Japan and China, but it is much the most widely cultivated of all Cycads, and specimens may be found in cultivation all over the world. Its natural habitat is in open, sunny, well-drained situations (Fig. 711).

FIG. 711.—*Cycas revoluta* growing on a hillside in southern Japan.
(*From a lantern slide lent by Professor Chamberlain.*)

GENERAL MORPHOLOGY

When young the stem is almost tuberous, its apex sheathed in brown scales and bearing a cluster of pinnate leaves 3 or 4 ft. long, and of hard, leathery texture. The pinnae are closely set on the rachis and there is no terminal pinna (Fig. 712).

Growth is very slow, but in course of time the stem builds up a thick, columnar trunk which is normally unbranched, except in certain cultural varieties which produce lateral adventitious buds. The plant lives to an age of several hundred years, and very old specimens with trunks nearly a metre thick are known in the wild state.

The old stem is sheathed in a hard armour of woody leaf bases, which persist for many years, and as the leaves are formed in a close spiral succession the bases cover the stem surface completely, as in the Male Fern. The primary root persists as a tap root. It is often short and tuberous, and may be as thick as the stem itself.

A new cluster of leaves is formed each year, but the old leaves are not immediately dropped, so that most plants have leaves of at least two years present at any given time. The new leaves are formed at the apex in continuous succession with the old leaves, and they develop during a whole year under cover of the armour of scales round the apex. When they push the scales aside and begin to open out, growth is very rapid and they may reach full size in a few days. In *Cycas* the main rachis is incurled (circinnate) and the pinnae are inrolled, as in the Ferns (Fig. 713). In *Zamia* the main rachis is incurled, but the pinnae are straight. This inrolling of the developing leaf is a definitely Filicalean character.

The scale leaves which cover the apex, and under cover of which the foliage leaves develop, are formed periodically in series with the leaves. Every year, or every second year, a group of new leaves is formed, and in the interval the succession is kept up by the formation of scales. The scales, like the leaf bases, are persistent and form part of the armour of the old stems.

FIG. 712.—*Cycas revoluta*. Single leaf. The one-foot rule shows the size.

A striking peculiarity of *Cycas* is the formation of small bunches of dwarfed apogeotropic roots, just below ground level (Fig. 714). These so-called "coralloid" roots are not unlike the nodular roots of *Alnus*, except that they grow upwards into the air. They are stumpy, dichotomously branched and closely massed, and like those of the Alder they usually contain an endophyte, which in this case is a Blue-green Alga, *Anabaena cycadacearum*. The Alga inhabits a zone of large disorganized cells in the inner cortex (Fig. 715), but it does not seem to be responsible for the singular form of these roots, as they are sometimes found without it. Whether any form of symbiosis is involved is not known, but Bacteria are also present, which suggests that Nitrogen fixation may occur, as in the root nodules of the Leguminosae.

ANATOMY OF THE STEM

The stem anatomy of *Cycas* is relatively simple. The meristematic tissues of the apex are not separated into distinct zones (Fig. 716). There is a primary ring of narrow vascular bundles, which is usually small in comparison with the diameter of the stem (Fig. 717). The greater part of the bulk,

FIG. 713.—*Cycas revoluta.* Circinate vernation of leaves. (*After Chamberlain.*)

FIG. 714.—*Cycas revoluta.* Group of coralloid roots.

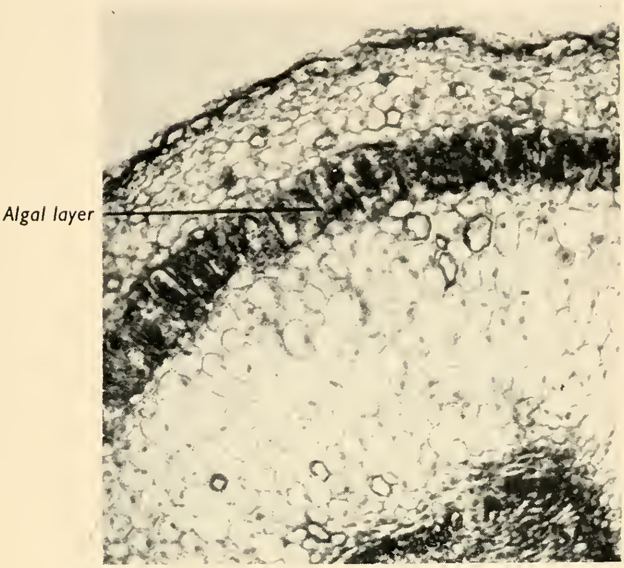

FIG. 715.—*Cycas revoluta.* Transverse section of a coralloid root showing the zone of cells inhabited by *Anabaena cycadacearum.*

even in old stems, consists of parenchymatous cortex, the cells of which are densely filled with starch grains. This ground tissue is traversed by numerous mucilage canals. The rigidity of the trunk depends, therefore, largely on the highly sclerotic armour of leaf bases already mentioned. This is additionally fortified by the formation of corky periderm outside the cortex, so that the armour and periderm together may be 10 cm. thick. This periderm is first formed in the leaf bases themselves, successive phellogens appearing, centripetally, until the leaf base is finally cut off at the level of the stem surface. Then another phellogen appears in the outer cortex,

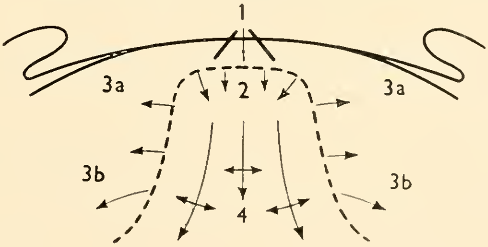

FIG. 716.—*Cycas revoluta.* Diagram of the meristematic tissues at the stem apex. 1, Group of initial cells. 2, Corpus cells. 3a, Tunica layer. 3b, Cortex developing from the flanks of the corpus. 4, Medulla developing from the corpus. The arrows show the directions in which differentiation is taking place. (*After Adriance Foster.*)

producing a corky bark which replaces the outer armour of leaf bases and finally forms the stem surface in the lower part of the oldest plants. In some other species the leaf bases are never lost and the age of the plant may then be gauged by counting them.

Secondary thickening is not vigorous. In *Zamia*, *Dioon*, *Stangeria* and *Ceratozamia* there is only one ring of vascular bundles, which slowly increase in size radially by means of cambium. As the bundles increase in size the medullary rays between them become so narrowed that the wood appears to form a continuous ring. In *Dioon* the wood may show rings like annual rings, which are, however, formed at irregular intervals. Only in rare cases does the zone of secondary wood reach any considerable thickness. This is called the **monoxylic** type of stem. *Cycas*, *Macrozamia*, *Encephalartos* and *Bowenia* start by being monoxylic but later develop several successive vascular rings, concentric with the first, and are therefore **polyxylic** (Fig. 718). The cambium of the first ring remains active for only a short time and is succeeded by another which is formed independently in the pericycle or cortex. This again is superseded by a third. As many as fourteen rings have been found. Usually the xylem and phloem of each ring are normally orientated. In *Macrozamia*, however, a tertiary ring with inverted orientation may appear between the first and second rings, and in *Cycas* occasional arcs of inverted bundles may occur between the normal rings. This may indicate a partial reversion to a structure with concentric bundles and has been held to indicate

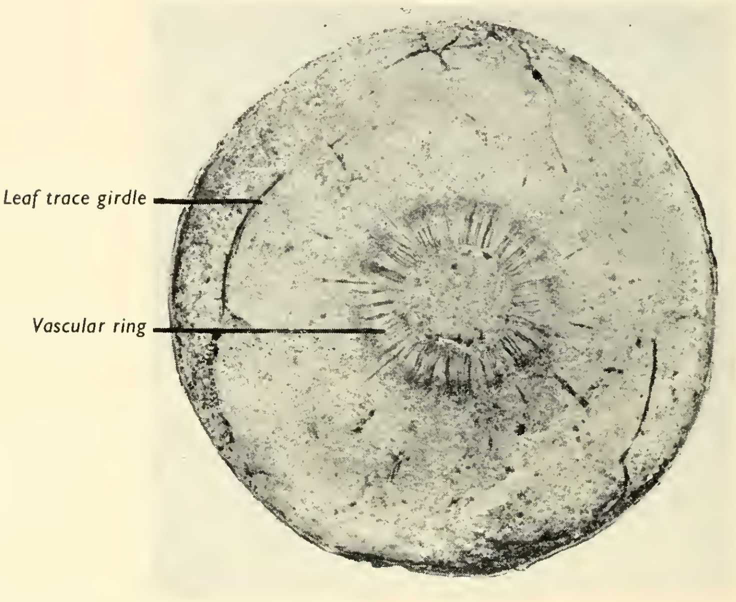

FIG. 717.—*Zamia floridana.* Transverse section of young stem showing large cortex containing girdle bundles and small vascular ring with numerous medullary rays.

a derivation from the fossil Medullosae, where the vascular system may consist of a group of concentric steles. There are no vessels present in the wood. The protoxylem consists of spiral tracheids, but the metaxylem has bordered pits in several alternating rows on the radial walls. This is the type known as araucarioid, which is also found in *Cordaites*.

FIG. 718.—*Cycas revoluta*. Transverse section of part of a polyxylic stem showing two of the concentric rings of vascular tissue.

The medullary rays are at first fairly broad and deep, so that the wood has the same loose character that is seen in the Pteridosperms. The phloem is broad and contains sieve tubes, parenchyma and fibres.

A striking feature of the stem anatomy is the "girdling" of the stem by the leaf traces. Each leaf is supplied by two main trace bundles, which arise by the branching of one trace which springs from the primary vascular cylinder on the opposite side of the stem from the insertion of the leaf. This trace springs from the inner edge of the primary xylem and passes out of the ring through a gap formed by the splitting of a vascular bundle.

The trace first passes obliquely outwards through the cortex, then it divides and the two halves diverge, each running round in opposite directions in the outer cortex, gently rising and meeting at the base of the leaf, where they bend sharply out into the petiole. These are the **girdle bundles.** In their course they cross the girdle bundles of each of the other leaves in their own group, and there is a distinct gap longitudinally between the girdle systems of successive leaf groups, which are, however, linked by anastomosing bundles. Leaf traces, called **radial traces,** also arise from other points around the vascular ring. These also bifurcate, and each half produces a complex system of anastomosing branches, which are attached to the girdle bundles both of their own and of other leaves in the same group. The leaf traces of each group of leaves thus altogether form a single united system.

FIG. 719.—*Liriodendron tulipifera.* Model of the vascular structure at a stem node showing girdle development of the leaf traces. The upper leaf trace bundle gives off short stipular traces.

The two girdle bundles, each augmented by additions from the radial bundles of the system, enter the leaf base and there they branch freely, the separated branches arranging themselves in the horseshoe pattern characteristic of the petiole.

A somewhat comparable system of leaf traces occurs in *Liriodendron* and some other members of the Magnoliaceae, a fact which may possibly indicate a Cycadean relationship for this group of Angiosperms (Fig. 719). As in Cycads the girdling is absent from the flower structures.

The xylem of the girdle bundles faces inwards. They are usually of collateral structure, but in *Cycas* concentric bundles occur, each with its own pith, xylem ring, cambium and outer phloem ring. The xylem elements differ from those of the stem bundles in being scalariform, as in Ferns. As these girdle systems are permanent, they must expand in conformity with the secondary growth of the stem, and their xylem elements become progressively longer as the stem grows. These girdles must play no small part in strengthening the trunks of old plants. It is noteworthy that in the seedling there is no girdle system and the leaf traces take a direct course from stele to petiole. This is probably the more primitive arrangement. Girdles are also absent from the cones.

A leaf trace at its point of entry to the petiole is normally collateral, with the xylem on its upper side, as in the Conifers. The xylem consists of regular rows of tracheids separated by medullary rays and is partly primary, partly secondary in origin, but is all centrifugal, with an endarch protoxylem. Higher up the petiole, however, this xylem gradually diminishes and another, centripetal, mass of xylem appears on the other side of the protoxylem (Figs. 720 and 721). Throughout the greater part of the frond the bundle contains a large mass of this centripetal xylem with only a small remnant of the centrifugal wood, which is separated from the protoxylem by parenchymatous cells. Bundles with both types of xylem are well known among Vascular Cryptogams, but are otherwise almost unknown in Spermatophytes. They are called mesarch (Fig. 722). In the Cryptogams, however, both xylems are primary, while in *Cycas* it is not certain that the centrifugal xylem in the petiole bundles is truly primary. It may be at least in part a remainder of the secondary xylem of the trace bundle. In *Stangeria* it does seem to be truly primary, but in other Cycads the term mesarch may not properly be applied as that signifies a homology with the cryptogamic type which is unproven. The term **diploxylic** is preferable.

ANATOMY OF THE LEAF

The lamina of the *Cycas* leaf is leathery and thickly cutinized. The epidermis and the upper hypodermis are highly thickened, and the stomata, on the lower surface, are sunk in pits with overarching rims. The mesophyll has a well-developed palisade layer on its upper side and the lower part of the mesophyll consists of parenchymatous cells with rather scanty intercellular spaces, corresponding to the spongy mesophyll in Angiosperms (Fig. 723). Between the palisade layer and the lower mesophyll there is a layer, three or four cells thick, of long colourless cells which run transversely from the midrib to near the margin. As the midrib is unbranched these cells probably form a conducting channel for water and are called the **transfusion tissue** (cf. *Pinus*, p. 673). The whole external aspect of the leaf is similar to that of some Palms with which Cycads were originally classified on account of this superficial resemblance.

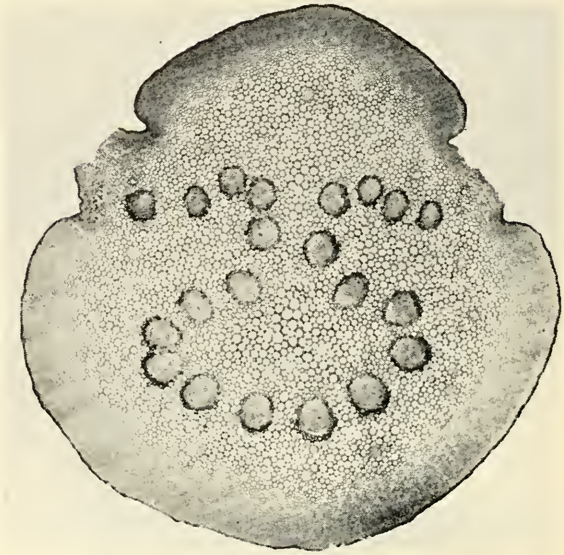

FIG. 720.—*Cycas revoluta.* Transverse section of a petiole showing numerous vascular bundles in a convoluted arc.

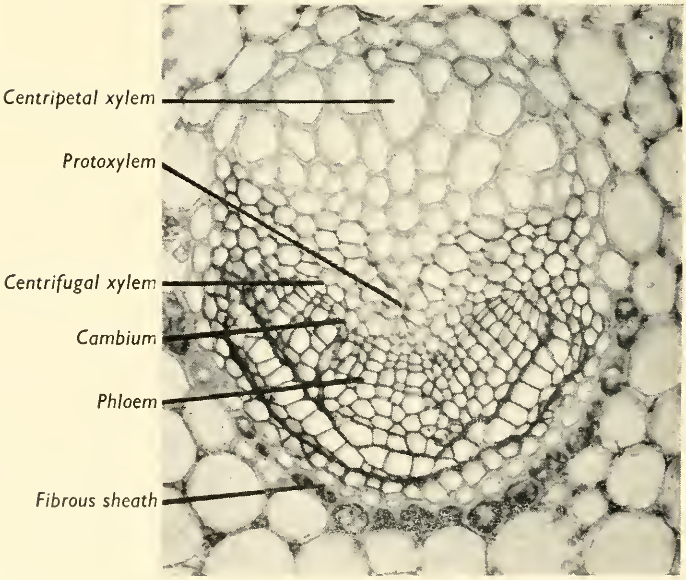

FIG. 721.—*Cycas revoluta.* Transverse section of a single bundle from the upper part of a petiole showing the considerable development of centripetal xylem and diminution of centrifugal xylem.

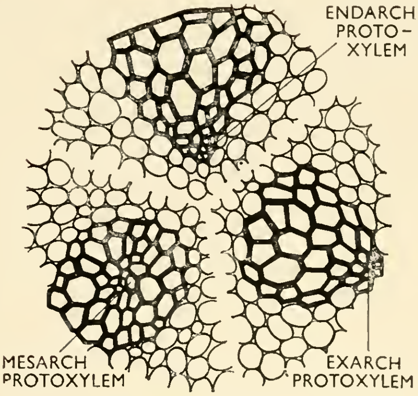

Fig. 722.—Diagram to illustrate the difference between the exarch, endarch and mesarch positions of the protoxylem. (*After Zimmermann.*)

Fig. 723.—*Cycas revoluta.* Transverse section of a pinna showing the palisade tissue and the transversely elongated transfusion cells in the lower mesophyll.

Anatomy of the Root

The coralloid roots have been described above. The structure of the primary tap root is very like that of a fleshy Dicotyledon (Fig. 724), diarch in its youngest parts and becoming polyarch near the base. Old roots have several concentric vascular rings which develop simultaneously with the same structures in the stem and they also develop a periderm. A root cap is present, but it arises from the periblem and there is no true calyptrogen layer. The branching of the lateral roots has the appearance of dichotomy, but this arises from the arrest of their apices and the development of opposite lateral roots close to the arrested apex.

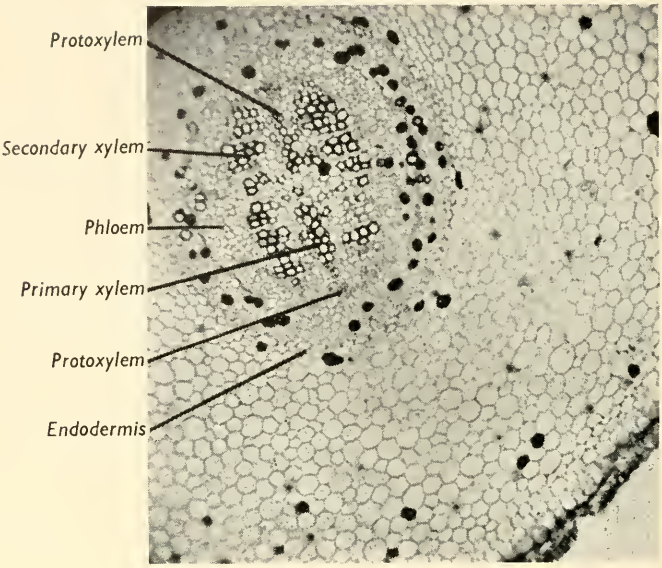

FIG. 724.—*Cycas revoluta.* Transverse section of a young primary root showing diarch primary xylem separated from the early secondary xylem by parenchyma.

REPRODUCTION

The cones of *Cycas* are terminal on the main stem, the sporophylls being formed spirally in succession with the foliage leaves. In the female strobilus the vegetative apex is not affected and continues its growth directly through the cone, but in the male an axillary bud is formed at the base of the cone which displaces it laterally and becomes the new stem apex. This is also the usual case in other Cycads.

The vascular supply to the male cone takes the form of a ring of bundles arising from the inner edge of the main vascular cylinder and converging like a dome towards the base of the peduncle. Successive peduncular domes may be seen in the pith in longitudinal sections of old stems.

THE MALE CONE

The **microsporophylls** are arranged in a close spiral on the male cone, which may be 50 cm. long (Fig. 725). They are woody in texture, wedge-shaped and blunt-ended. The lower surface of each is continuously covered with **microsporangia** (pollen sacs) (Fig. 726), but closer inspection shows that they are really grouped into **sori** of from three to six sporangia, arising from a central papilla, to which the dehiscence slits are radial. The analogy with *Marattia* is here fairly obvious, and indeed the grouped, or alternatively, synangial arrangement of the microsporangia is a common feature which helps to link Marattiaceae, Cycadales, Bennettitales and Medullosae together into one related plexus. The resemblance to *Marattia* is increased by

FIG. 725.—*Macrozamia miquelii.* Part of a male cone opened to show the microsporangia on the under surface of the sporophylls.

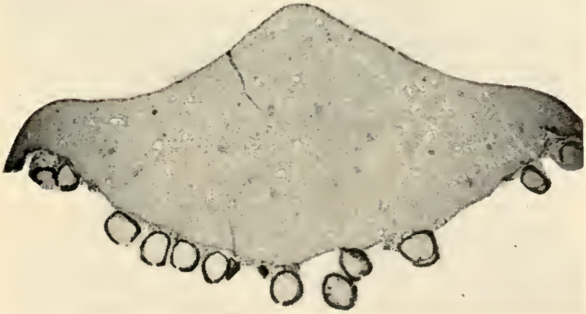

FIG. 726.—*Encephalartos sp.* Transverse section of a microsporophyll showing mucilage ducts and microsporangia scattered on the lower surface.

the presence of a zone of indusial hairs arising from the papilla below each sorus.

There may be several hundred sporangia on each sporophyll and several thousand spores in each sporangium, so that the spore output is very large.

This agrees with the relatively primitive structure of *Cycas*, a smaller output being characteristic of the more specialized forms, such as *Zamia*.

Each sporangium develops around a single **archesporial cell**, which arises in the hypodermis of the sporophyll. The sporangial wall is massive and several layers thick. Its epidermis later becomes highly thickened and two rows of elongated cells mark the line of dehiscence. There is a scanty **tapetum** which shrivels up at maturity along with all the inner layers of the wall called collectively the **endothecium.**

The mature sporangium is oval and attached by a short stalk at one end. The dehiscence is longitudinal, as in Marattiaceae, and as in the latter there is no organized annulus. The outer thickened layer of the wall, the **exothecium,** indeed, functions as a generalized annulus, which shrinks with the loss of water from its cells and causes the splitting open of the wall along the abaxial side, where the cells are smaller and thinner, so that the open sporangium becomes boat-shaped and the spores easily fall out. The cells of the exothecium on the adaxial surface are thinner walled than those below and act as a contractile " hinge " in the opening of the wall. Functionless stomata are present near the base of the sporangium, recalling the foliar nature of the sporophyll from which it arises, the epidermis of which is continuous with the exothecium. Sporangial stomata have, however, been lost in all other Gymnosperms and in the Angiosperms.

Each **spore mother cell** at meiosis forms a cell with four lobes separated by thickened partitions, and inside each lobe of this structure a **microspore** develops.

The microspore has two spore coats with thickenings at opposite poles. The **extine** is thickest at one end and tapers gradually towards the other end of the spore. The **intine** is thickest at the sides. Germination begins before the liberation of the spore. A lateral **prothallus cell** is cut off, which persists. The remainder of the cell divides again forming an **antheridial cell** attached to the prothallus cell and a **tube cell** with a very large nucleus. At this stage the spore is shed. The spores are light and dry, and field observations support the view that they are wind borne.

The Female Strobilus

The **megasporophyll** of *Cycas revoluta* is one of Nature's curiosities. It preserves in a living Seed Plant the image of the seed-bearing fronds of the Palaeozoic Pteridosperms. There is no properly organized cone, only a crown of sporophylls formed seriatim with the leaves, in acropetal succession (Fig. 727), leaving the apical meristem unaffected, to grow on and form future leaves and sporophylls. Young plants do not produce sporophylls, and the growth of *Cycas* is so slow that it may be many years before the plant reaches maturity, but after it arrives at that stage sporophylls are formed each year between successive crowns of foliage leaves. They are far more numerous than the leaves, and their persistent bases contribute more to the stem armour.

FIG. 727.—*Cycas revoluta.* Apex of a flowering plant showing the apical cluster of megasporophylls with attached ovules.
(*From the "National Geographic Magazine."*)

Each sporophyll is 6 to 8 in. long, the upper portion broadly pinnate, like a leaf, and tapering to a point (Fig. 728). On the lower half are two lateral rows of orange-coloured ovules, apparently replacing the pinnae on this part of the organ. The whole structure is covered densely with brownish hairs, but these are lost from the ovules as they ripen.

Other species of *Cycas* show traces of pinnate structure in the sporophylls and a reduction series may be arranged starting from *Cycas revoluta* and showing all stages in the modification of the megasporophyll, from a structure in which the semblance of a leaf is still evident, to a short woody structure in which all foliar semblance has been lost, forming part of a cone as closely built as that of a Pine (Fig. 729). Such a series probably does typify the actual course of evolution of the cone in the Cycadales, but it leads into a cul-de-sac, and the ancestors of the Angiosperms probably had more in common with the loose organization of *Cycas revoluta* than with the high specialization of types like *Zamia.*

The **ovules** are the largest in the plant world. They increase but little in ripening and may be as large as a hen's egg. They are slightly flattened in the plane of the sporophyll, and this shape corresponds to a dorsiventral

FIG. 728.—*Cycas revoluta.* A single megasporophyll showing pinnate apex and two rows of laterally attached ovules.

internal structure. The essential difference between the ovule of a Seed Plant and the megasporangium of a Cryptogam is that the former is enclosed by an **integument.** In *Cycas* the integument is massive and consists of a stony layer with fleshy layers both outside and inside it. Although three-layered it seems to be all one structure. There is a narrow **micropyle** with a small micropylar beak.

The megasporophyll traces come directly from the stem stele, without girdles, and the vascular supply to the ovules comes from one of the collateral mesarch bundles in the rachis of the sporophyll. This turns out into the ovular pedicel and there it becomes concentric, with a solenostelic structure and some centripetal xylem. This stele forks into two at the seed base, each portion retaining the concentric structure and being surrounded by a distinct bundle sheath and by what seems to be transfusion tissue, as well as having minor accessory strands surrounding it. The further development of the seed supply is shown in Fig. 730. The vertical plane in the figure is the greater diameter of the seed and is known as the **principal plane.** The stony layer is shown by a hatched zone, and it will be seen that two branches from the outer group of bundles pass through the base of the stony layer and join the central bundle to form the supply bundles to the inner fleshy layer of the integument, which they traverse to its apex, with slight branching. The

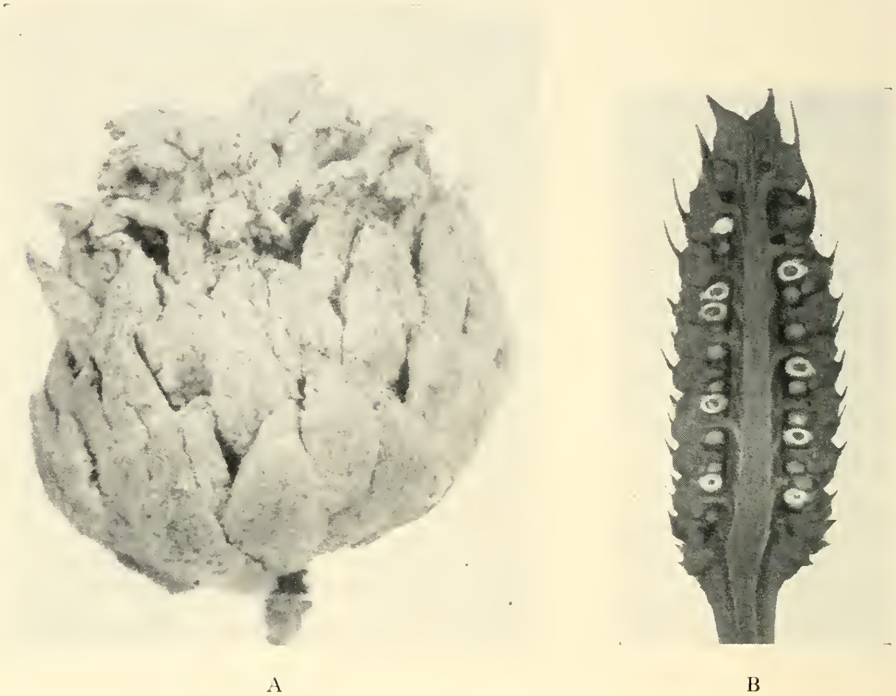

FIG. 729.—Types of female cones. A, *Dioon edule* with loosely arranged foliar sporophylls. B, *Macrozamia miquelii* with closely arranged peltate sporophylls and pendant ovules shown in longitudinal section.

central bundle ends in a tassel of branches below the nucellus. The bundles outside the stony layer do not branch but pass upwards through the outer flesh to the micropyle. This structure should be compared with that described under *Taxus*, where the correspondence with some of the fossil seeds is pointed out. The existence of this concentric structure in the seed pedicel is of great interest as a link with the fossil Bennettitales, in which the seed pedicel contains a single concentric strand which passes upwards into a circular zone of transfusion tissue surrounding the ovule.

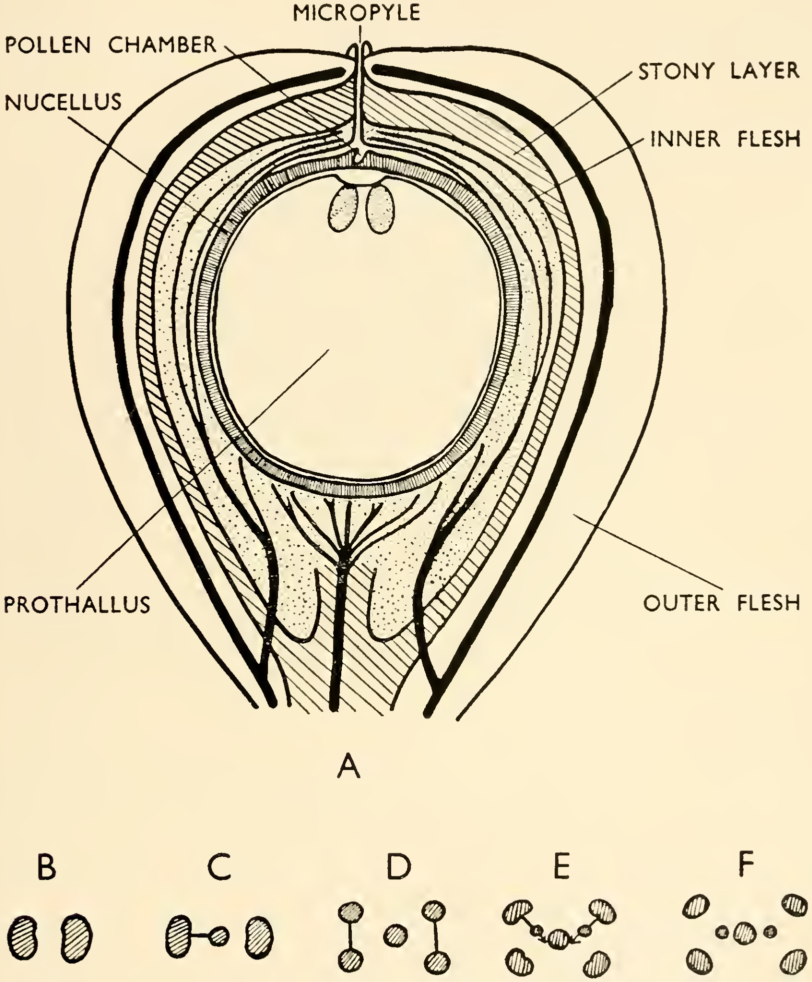

FIG. 730.—*Cycas revoluta*. Structure of the seed. A, Longitudinal section of the seed with vascular bundles shown in black. B to F, Vascular supply to the seed as seen in a series of transverse sections of the pedicel, in succession from below upwards. F is through the base of the seed. (*After Stopes.*)

The early development of the ovule has not been fully studied in *Cycas*, and we can only state what has been found in related genera. At an early stage the integument is fleshy throughout and the nucellus is united to it, except near the apex. When the ovule is ready for pollination, the gametophyte being still undeveloped, the apex of the nucellus grows up into the micropyle as a beak, and some of its cells break down to form a flask-like hollow called the **pollen chamber**, which plays an important part in the preliminary stages of fertilization (Fig. 731).

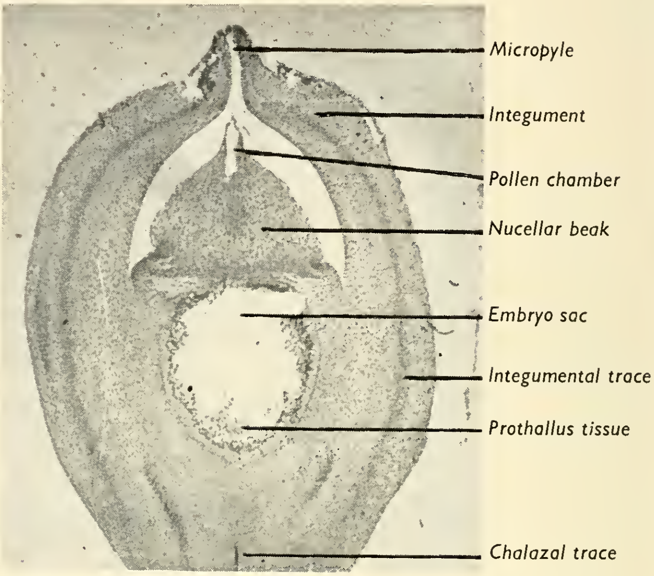

FIG. 731.—*Stangeria paradoxa.* Longitudinal section of the ovule.

By the time the archesporial cell is distinguishable the nucellus is well grown. This cell divides to form a row of three or four cells, of which all abort except the lowest, which becomes the **megaspore.** As it enlarges the surrounding cells of the nucellus take on the character of " spongy tissue," as described in *Pinus.*

THE FEMALE GAMETOPHYTE

In the formation of the **prothallus** there is a prolonged period of free nuclear division in the young megaspore, the nuclei being forced outwards by the growth of a large central vacuole to form a peripheral layer around the wall of the cell. More than 1,000 nuclei may be formed before walls begin to appear. The development of the prothallial cells is centripetal and probably similar to that in *Pinus.* When the whole space inside the megaspore has become filled with tissue the cells develop numerous starch grains, except the outermost layer of small cells. The outer wall of the megaspore thickens and persists as a solid megaspore membrane around the prothallus. It consists of two layers, the outer of which is suberized and appears finely papillate.

Soon after pollination several peripheral cells at the micropylar end of the prothallus begin to enlarge. These are the **archegonium initials** and they vary from two to eight, with three as the commonest number.

The initial cell divides transversely into a **neck cell** and a **central cell.** The former divides again vertically into two cells, which constitute the neck. The central cell enlarges to about 4 mm. long and forms the **oosphere** cell. At first its protoplasm is scanty and the centre is occupied by a large vacuole. When this growth phase is over the protoplasm increases and fills the whole cell, the vacuole disappearing. The oosphere cell wall becomes thick and amyloid and develops open pits connecting with the adjacent prothallial cells. These cells are organized as a special **jacket layer,** and from them food materials pass into the oosphere cell with which their protoplasm is connected through the large pits. The turgidity of the oosphere cell is so great that its cytoplasm protrudes into the jacket cells as " haustoria," and eventually absorbs all the contents of these cells. The cytoplasm of the oosphere cell becomes very dense and turbid, and contains starch, oil and protein reserves. This nutritive phase lasts from two to three months.

Finally the nucleus of the oosphere cell divides, forming a short-lived **ventral canal nucleus** and an **oosphere nucleus,** which enlarges until it may be half a millimetre across and visible to the naked eye. Its chromatin becomes hidden by other contents, probably reserve protein. The archegonium is now ready for fertilization. The prothallus tissue around the archegonium grows upwards and forms a shallow basin, the **archegonial chamber,** in which the archegonial necks lie (Fig. 732). The megaspore membrane is ruptured above the chamber, and the bottom of the pollen chamber in the nucellus also becomes disorganized, so that a free passage to the archegonia is opened for the pollen. A drop of mucilaginous fluid fills the micropyle and exudes as a pollination drop outside the ovule. In this the pollen grains are caught and, as it dries up, are drawn down into the pollen chamber. There the pollen grains are sealed in by the dried liquid.

The Male Gametophyte

The pollen germinates in about a week after pollination. The **antheridial cell** divides into a **stalk cell** and a **body cell** which together represent an antheridium. A pollen tube grows out from the thin-walled apex of the microspore, but this is not an agent of fertilization as it is in Angiosperms. It is simply a nutritive haustorium and it penetrates the nucellus laterally, gradually digesting and breaking down tissues above the archegonial chamber.

No further development takes place until the archegonia are mature, a further period of about four months. The **prothallial cell** meanwhile penetrates into the stalk cell, reducing it to the form of a ring. When fertilization time approaches, the body cell enlarges enormously and two granular **blepharoplasts**, surrounded by radiating fibrils, appear in it, which take up positions transversely, one on each side of the nucleus. These blepharoplasts are concerned in the production of cilia, and they have their counterparts in many unicellular organisms and in some antherozoids of lower plants, but nowhere are they so large or complex as here.

The body cell divides between the blepharoplasts, and each half produces an **antherozoid**. Each blepharoplast breaks up into a cluster of granules, attached to a beak which grows out from the nucleus. The latter then rotates, drawing out the cluster of granules into a long spiral band from which thousands of **cilia** develop. The nucleus enlarges until it occupies nearly the whole of the antherozoid cell, the protoplasm of which rounds off and separates from the wall. This breaks down and liberates the contents into the body of the microspore as a fully motile antherozoid (Fig. 733). The male cells begin to move even before their liberation from the antheridial cell and they apparently remain motile for several hours. These antherozoids are the largest of all known male cells. They may reach a size of 250μ × 300μ and are visible to the naked eye.

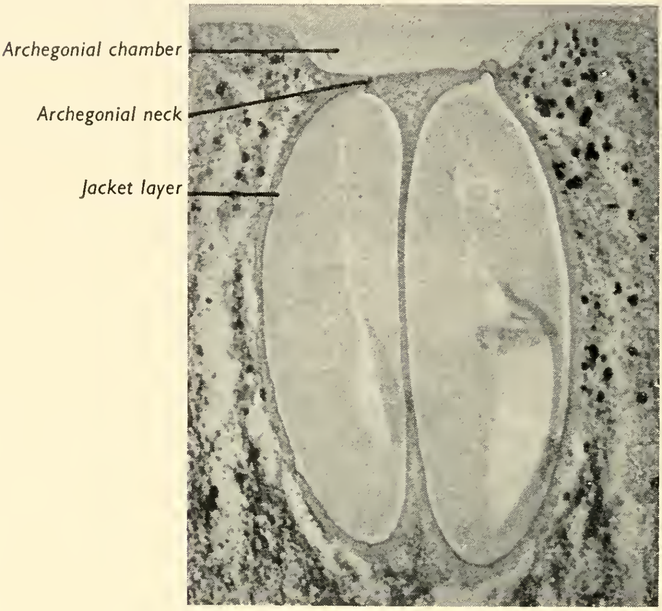

FIG. 732.—*Dioon edule*. Longitudinal section through the apex of the female prothallus showing a pair of archegonia.

FERTILIZATION

The basal end of the microspore now enlarges and forms an elongated sac which hangs down into the archegonial chamber. It is extremely turgid and contains highly concentrated fluids. Antherozoids will not live in sugar solutions of less than 30 per cent. strength, which indicates what the osmotic potential of the pollen sap must be. The swollen pollen sac bursts under this osmotic pressure and discharges its fluid contents with the antherozoids into the archegonial chamber. The strong fluid draws water from the archegonial neck cells and from the oosphere, in which vacuoles appear. When an antherozoid touches a neck cell it is sucked violently into the oosphere, the cytoplasm and blepharoplast are stripped off, and the naked nucleus approaches and unites with the oosphere nucleus.

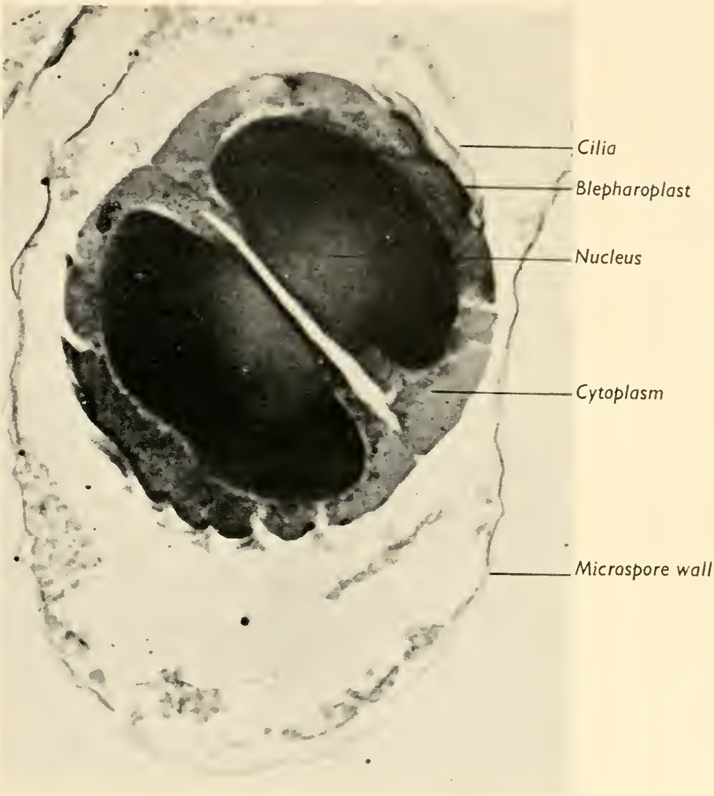

FIG. 733.—*Ceratozamia mexicana.* Portion of a microspore showing the antheridial body cell dividing to form two antherozoids with very large nuclei.

EMBRYOGENY

As in *Pinus*, and apparently in Angiosperms, the chromatin of the two nuclei does not immediately fuse, and when division begins there are two spindles formed, which merge into one. Only the monoploid number of chromosomes can be counted, and the explanation is probably the close pairing of male and female chromosomes which makes them indistinguishable.

The early divisions of the oospore nuclei are free and simultaneous and two to three hundred nuclei are scattered throughout the oospore. The period of free nuclear division continues longest at the base of the oospore, and it is from this region that the suspensor and embryo arise. Following this period there comes a simultaneous formation of cell walls throughout the oospore, but all the central cells break down leaving a large cavity with one or two cell layers round the outside. The first differentiation is that of the suspensor cells near the base of the oospore, which elongate immensely, pushing the lowest group of cells through the oospore membrane and right down to the base of the prothallus. All the archegonia may be fertilized, and each oospore may produce a suspensor. These all twist together and form a compound structure supporting the one embryo which develops to maturity. The coiled suspensors may be pulled out to a length of several centimetres and their function seems to be simply to thrust the embryo into the middle of the nutritive prothallus tissue. The tough oospore membrane remains persistent for long after the embryo has grown and may be pulled out of the ovule with the suspensors. Development is slow, and when mature the embryo reaches the whole length of the seed. The suspensor is pushed back and packed against the micropylar end.

There are two cotyledons, sometimes unequal, and the embryo is perfectly straight. The mature seed coat consists of the hard, stony integument with its outer fleshy covering, the inner flesh having dried up. It encloses the female prothallus, which functions as a nutritive **endosperm,** and the straight embryo. The base of the embryo at the root end is marked by the development of a massive hard pad, the **coleorhiza,** partly formed of the suspensors, which appears even before the root itself is differentiated. It acts as a protection while the expansion of the embryo is breaking open the hard shell of the seed at germination, and it then turns papery and is pierced by the emerging root.

Germination

Cycad seeds have no resting period. They germinate directly, and never in any case keep their vitality for more than a few months. This points to a primitive condition of the seed as compared to some of the highly persistent seeds of Angiosperms. The cotyledons remain in the seed coat, below ground, and continue active as long as there is any endosperm left for them to absorb ; when this is finished they dry up.

The seedling stem is very short indeed, and its vascular system forms a plate rather than a column. At each of its four corners is a protoxylem, from which strands descend to form the vascular poles of the tetrarch root. Two of these may be suppressed in cases where the root is only diarch, and in any case two of them usually develop further than the other pair, so that the root becomes diarch near its tip. From the same protoxylems four strands pass upwards and forthwith divide. They go to the two cotyledons, each of which receives four. It will be realized that this seedling structure is an autonomous organization, complete in itself, and the solid vascular plate is the only truly cauline stele the plant possesses at any stage. Above this level the meristem organizes only leaf traces and the typical vascular cylinder is built up by their convergence in the central region. The first four sets of leaf traces are directly connected to the vascular plate, but the subsequent sets of traces arise from the preceding traces. This is the familiar pattern of the Dicotyledon stem where, however, the protostelic seedling plate has disappeared and leaf and root strands are directly linked to one another. Here, in this seedling plate, seems to lie the last relic of the extensive cauline stele of the Vascular Cryptogams, and above the Cycad level in the story of plant evolution we are faced with a new method of stem organization from leaf traces or " vascular bundles " which cannot be directly compared with the stelar organization of the lower plants. The flexibility of organization possible with the new method has evidently been a great gain, and it is not too much to say that the successful development of the Seed Plants has largely depended upon it. The fossil evidence shows that grafting the seed habit upon a cryptogamic vascular system did not succeed.

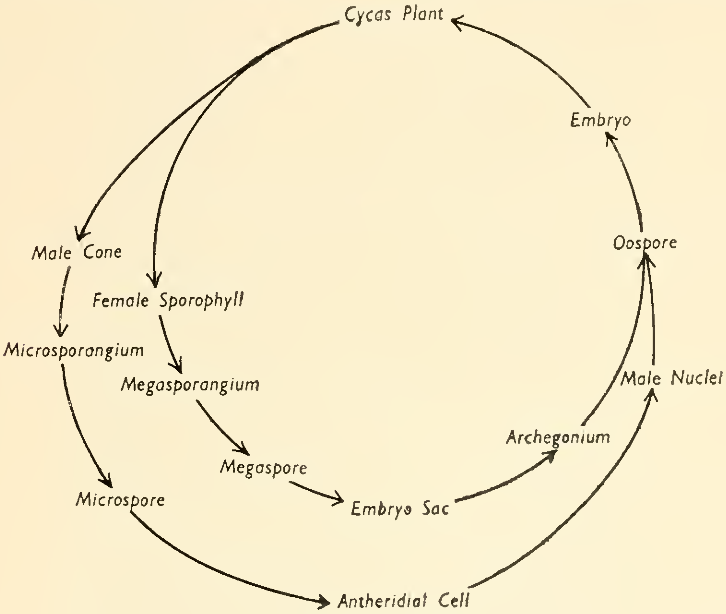

FIG. 734.—Life-cycle of *Cycas revoluta.*

Ginkgoales

There is only one living type included in this order, the species *Ginkgo biloba.* The characters of the order are therefore those of the species. Like *Cycas* it retains the cryptogamic character of fertilization by antherozoids.

Ginkgo biloba (The Maidenhair Tree)

This species has a good claim to be regarded as the senior living plant. Its peculiar leaves are found with certainty in the Permian, and with probability in the Carboniferous. It survived in Britain until the middle Tertiary. During the Jurassic period it reached its greatest abundance and almost world-wide distribution, aided probably by the prolonged resistance of the seeds to immersion in sea water, but it has declined progressively since that time and is now only found apparently wild in one or two places in the mountains of western China. Indeed until 1899 it was known only as a cultivated plant in China and Japan, where it has been grown from time immemorial as a temple tree (Fig. 735). Until the discovery of wild specimens it was supposed to have owed its preservation from extinction to this cause. Actually its popularity in the East has led to its being planted very widely elsewhere during the last two hundred years. It forms a graceful, strictly pyramidal tree, reported to reach nearly 100 ft. in China but rarely half that height in Britain. With age it acquires a rounded head by the upgrowth of the branches. It is quite hardy and is not uncommon in English gardens, where it forms a decorative small tree with fine autumn colouring. Most of the trees of flowering age in Britain are males, but the few females produce

Fig. 735.—*Ginkgo biloba.* A tree in a temple in western China.

(*From a photograph by E. H. Wilson.*)

seeds, as do also the female branches which have been occasionally grafted on to male trees.

The name *Ginkgo* is something of an etymological puzzle. It is supposed to be an erroneous copy of " Gin-ko," which is the Japanese equivalent of two Chinese symbols meaning " silver fruit," a reference to its plum-like fruits.

ANATOMY OF THE STEM

As in many Conifers there are both long and dwarf shoots, leaves being borne spirally on both. There is in fact no hard and fast line between the two types of shoot, and dwarf shoots may sometimes grow into long ones. It is largely a question of the relative rates of growth. Normally the spurs grow by very small increments to a length of 2 to 3 cm. and bear a cluster of leaves at their ends. Occasionally they may branch, even precociously within the wood of the axis from which they grow.

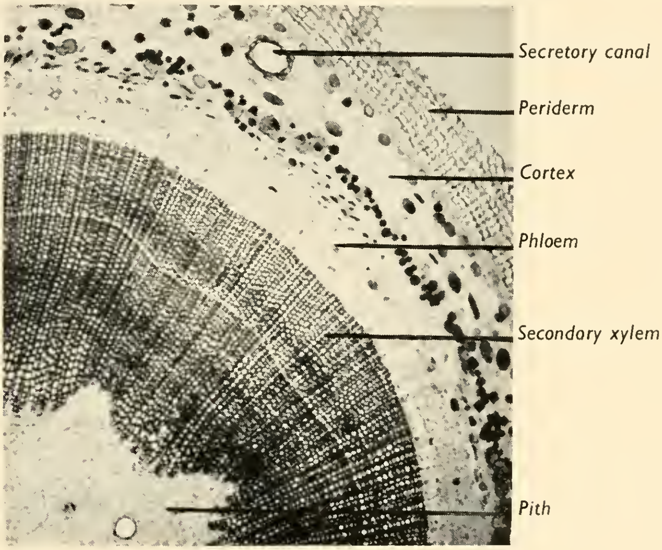

FIG. 736.—*Ginkgo biloba.* Transverse section of a two-year-old stem showing two annual rings in the secondary wood.

Anatomically the stem is of the *Pinus* type (Fig. 736). The protoxylem is formed of spiral elements which are exceptionally abundant, especially in the spurs. The later-formed tracheids are all of the bordered-pit type, with irregular pitting, often only in a single, loose row. There may also be two rows, either opposite or alternate, and, in the secondary wood, the thickenings known as Sanio's Rims are prominent between the pits. Here and there also are trabeculae, crossing the interior of the tracheids. These trabeculae have sometimes been confused with the Rims of Sanio, although the latter are thickenings in the cell wall itself.

The wood structure is therefore " abietinean," which is usually considered as a relatively advanced type.

Secondary thickening follows the same plan as in *Pinus*, but there is relatively little in the spurs. There is also an external phellogen and a heavy periderm, with a considerable growth of phelloderm, or secondary cortex, on the inner side of the phellogen. The medullary rays are exceptionally small, being almost invariably one cell broad and seldom more than three cells high, except in the spurs. Where they cross the tracheids they connect to them by large simple pits. Mucilage cavities are abundant throughout the tissues. There are annual rings, rendered evident, as in *Pinus*, by seasonal variation in the width of the tracheids, but not as a rule very prominent. The wood consists almost wholly of tracheids, but there is a small amount of xylem parenchyma containing Calcium oxalate crystals.

Outside the vascular zone is an imperfect ring of stone cells, probably pericyclic, accompanied by an inner ring of thickened cells, the walls of which seem to be gelatinized. Their function is unknown. In older stems the phloem is exceptionally broad and appears to be banded tangentially, owing to the collapse of rows of cells, between which the large sieve tubes are prominent. There are some discontinuous zones of fibres in the phloem and a small amount of parenchyma.

The stem structure of *Ginkgo* is in fact fundamentally much more akin to that of the Conifers than to that of the Cycads, though it differs in several details.

Anatomy of the Leaf

The leaves are the most striking feature of *Ginkgo* (Fig. 737). They are broadly fan-shaped, 4 to 7 cm. across, with a wavy margin and an apical notch which sometimes almost completely divides the blade into two portions.* Exceptionally there may be several notches, producing a palmatifid appearance, which is an interesting approach to the leaf structure of the related fossil genus *Baiera* and may be a relic of an originally compound leaf. The lamina tapers downwards into a flexible petiole which is often longer than the lamina itself. The leaves are produced in a spiral order, but on the spurs the internodes are suppressed, so that the leaves seem to spring from almost the same level. These spur leaves are usually undivided.

The lower margin of the leaf is thickened, the thickness increasing towards the petiole, so that the blade is really shaped like a flat spoon or scoop, recalling the " ascidial " or trumpet-shaped leaves which are found as abnormalities in many Angiosperms.

The petiole contains a double leaf-trace of two collateral strands which show secondary growth, surrounded by a sheath of thick-walled cells (Fig. 738). A similar double leaf-trace is found in some Pteridosperms, in Cycads

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* The resemblance of the leaf to that of the Maidenhair Fern, *Adiantum capillis-veneris* gave rise to the name by which *Ginkgo* was formerly known, *Salisburia adiantifolia*, and also to the English name.

and in *Cordaites.* On entering the blade the traces separate to right and left and then fork repeatedly, each half of the blade having thus an independent

FIG. 737.—*Ginkgo biloba.* A branch showing the characteristic leaf form.

venation. There are no side connections, so that if a vein is severed near the base of the leaf, the strip of tissue above, which should have been supplied

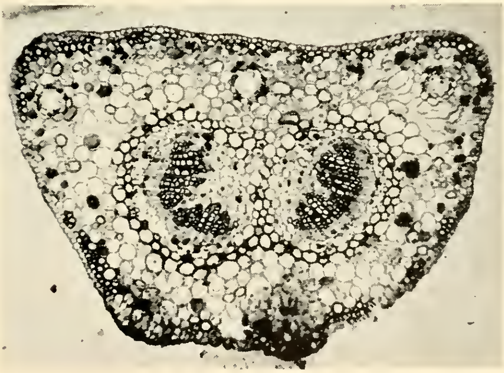

FIG. 738.—*Ginkgo biloba.* Transverse section of the petiole showing the double bundle.

by its branches, withers and dies. This has often been cited as evidence of the physiological superiority of net-venation, which gives ample provision of alternative passages for the water supply. No doubt theoretically this is true, but it must be pointed out that transverse tearing of the *Ginkgo* leaf is very difficult owing to its leathery texture, and that in Nature it does not seem to suffer at all either from this or from insect injuries to the foliage. On the other hand, this security is attained by an expenditure of material in leaf thickening, occasioned by the weakness of design, which should be unnecessary for a deciduous tree.

The vascular bundles of the leaf are collateral and are accompanied by short transfusion tracheids which increase in number towards the leaf margin and finally replace the ordinary xylem tracheids at the extremity of the vein.

The leaf traces in the stem are not girdled like those of *Cycas*, but they do not enter the vascular zone directly, passing instead obliquely downwards through the cortex for a distance of four internodes before they become part of the vascular ring. Here again, as in Conifers and Cycads, and indeed in all the Angiosperms, we have to do with a vascular system which is composed of leaf traces. There is no portion of the system peculiar to the stem.

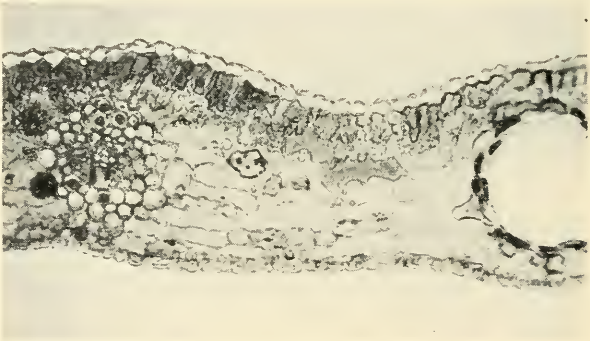

Fig. 739.—*Ginkgo biloba*. Transverse section of the lamina showing irregular palisade cells and transversely elongated mesophyll. On the left a vascular bundle, on the right a mucilage canal.

The mesophyll of the leaf blade is only differentiated into palisade and spongy layers in the leaves of the long shoots (Fig. 739). In the spur leaves the mesophyll is practically uniform, except that the loose cells of the middle tissue are drawn out parallel to the leaf surface (cf. the transfusion tissue in *Cycas*). Long mucilage canals may be seen like dark streaks between the veins.

Although the leaves are **deciduous**, that is, are dropped in winter time, they are rather hard in texture and have a thick cuticle and sunken stomata on the lower surfaces, characters which mark them as **xeromorphic**, like those of *Pinus*.

The stomata are surrounded by small **accessory cells** which project inwards over the stomata in a very characteristic way, which can be recognized also in fossil members of the order.

The buds of *Ginkgo* are covered by corky, not resinous, bud scales, and during the spring growth the inner scales develop a small petiole and lamina, so that, as in many Angiosperms, one can trace a series of intermediate forms connecting the smallest bud scales with the fully developed leaves.

Although the mature parts of *Ginkgo* are almost completely devoid of hairs, the petioles of young leaves and the bud scales are densely hairy, as in *Cycas*, and some hairs remain at the base of the petiole even in the mature leaf.

ANATOMY OF THE ROOT

There is little about the root structure that is different from that in the Conifers, except the very early differentiation of tissues at the apex. There is a persistent tap root, and the vascular structure of the young root is usually diarch. The details of the vascular tissues are closely similar to those of the stem.

THE MALE STROBILUS

As has been already mentioned, *Ginkgo* is dioecious. The male tree is said to be more upright in growth than the female, but it is doubtful whether this is always so. The male strobili are borne in the axils of leaves on the spurs, about half a dozen on each spur, so that the aggregate number for the tree is enormous (Fig. 740). They are about 1 in. in length and consist of a slender axis bearing closely set sporophylls in spiral order and without bracts. Each sporophyll normally bears two pendant sporangia at its apex, but three or four are occasionally present (Fig. 741). Above the sporangia is a prominent "hump" of sterile tissue containing a large mucilage cavity, and it has been suggested that this represents an additional sterilized sporangium.

FIG. 740.—*Ginkgo biloba*. Branches with spurs bearing young leaves and male strobili. (*From a photograph by Mr E. Cahen.*)

Against this, however, is the observation that when extra sporangia are developed they are on the under side of the sporophyll and that in such cases the hump is still present. The interest of the idea lies in this, that in *Baiera*, a Mesozoic fossil closely related to *Ginkgo*, the numerous microsporangia are arranged radially on the sporophyll, as in *Taxus*, and it was supposed that the hump on the upper side in *Ginkgo* might be a relic of this arrangement. However, *Baiera* also has a hump, at the end of the sporophyll, and when supernumerary sporangia occur in *Ginkgo* they are not radially arranged but are pendant, which somewhat damages the theory. The hump is in fact nothing more than a protective thickening of the sporophyll which covers the young sporangia during their early development.

The whole strobilus looks very much like a small catkin. Its axis contains a circle of nine or ten vascular bundles which gives off a double trace, of small collateral bundles, to each microsporophyll.

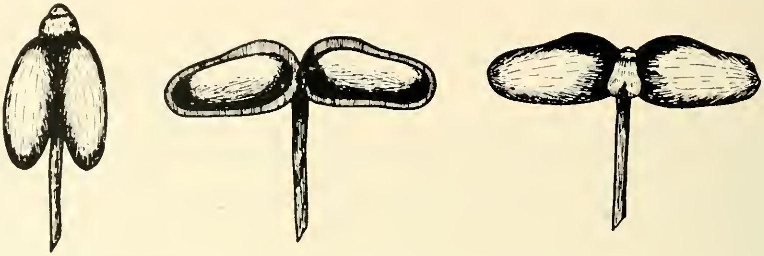

Fig. 741.—*Ginkgo biloba.* A male sporophyll showing on the left, the two sporangia and the sterile hump, and on the right the position assumed by the sporangia on dehiscence. (*After Pilger.*)

The sporangium wall opens by a longitudinal slit. Its structure is notable in that it is the middle layer of the wall, the **endothecium,** which bears cuticularized thickenings and is active in causing dehiscence. In this *Ginkgo* agrees with the Angiosperms and differs from other Gymnosperms, in which the outer layer or exothecium of the wall is the thickened, active layer.

The pollen grains are very like those of *Cycas* and the division of the contents to form prothallial cells begins, as in the latter, before the sporangium opens. Each grain has two little " ears " like miniatures of the wings on a *Pinus* spore.

Two prothallial cells are formed, the first of which aborts and later only shows as a thickening of the spore coat, as in *Pinus*. The second one persists. The remaining third nucleus divides again producing an antheridial cell, in contact with the prothallial cell, and a large tube-cell, which does not divide again. In this four-celled condition the pollen is shed.

THE OVULE

Ovuliferous shoots appear in the axils of the leaves or scales on the spurs of the female tree. A simple peduncle, about 1 in. long, bifurcates at its apex, each branch bearing one terminal, sessile ovule, the base of which is surrounded by a fleshy cup, the **ring** or **collar** (Figs. 742 and 743).

Much discussion has centred round this structure, for its morphological character is uncertain. It is usually referred to as the female "flower," but objection has been raised to this on account of its dissimilarity to any other flower type. The question, like many another, resolves itself largely into a matter of definition and, in consequence, much curious dialectic has been devoted to the attempt to analyse the botanical vocabulary. We shall have to consider the morphological nature of the Angiospermic flower in a future chapter, and it would be fruitless to go into it now. Furthermore the plan of trying to fit the structures of lower plants into the framework of ideas based upon higher plants has proved, again and again, to be wrong. *Ginkgo*

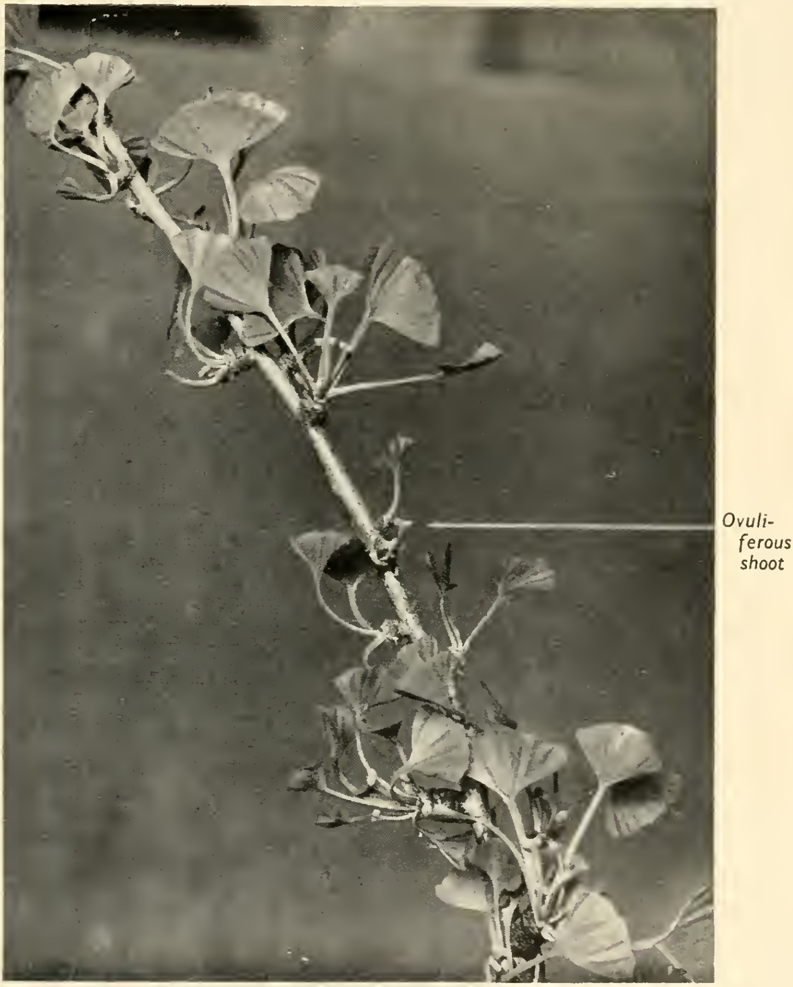

FIG. 742.—*Ginkgo biloba.* Branch bearing spurs with young leaves and ovuliferous shoots.

(*From a photograph by Mr E. Cahen.*)

is a Gymnosperm and therefore belongs to the class of Flowering Plants, but it is advisable to use descriptive terms for it which have as few theoretical implications as possible.

The structure in question is axillary to a leaf and is therefore by morphological axiom a branch or axis, not a simple sporophyll. Its anatomical structure agrees with this, so if we call it the **ovuliferous axis** we are stating nothing beyond the facts and keeping it in line with the treatment of the Pine cone.

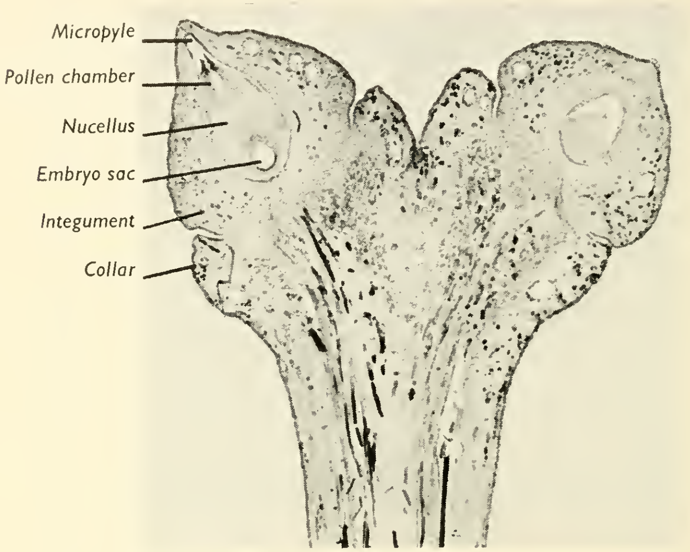

FIG. 743.—*Ginkgo biloba.* Vertical section through the apex of an ovuliferous axis showing the paired ovules each surrounded by a collar.

The foliage leaf and the male sporophyll have each two trace-bundles in their stalks. The ovuliferous axis has four (Fig. 744), which at once suggests that it is a double structure and that the two ovules represent two reduced sporophylls, the collar being perhaps a vestige of the individual sporophylls. Abnormalities are not uncommon in which several ovules appear on one common peduncle. Both the bi-ovulate and the multi-ovulate axes may also develop stalks to the individual ovules. Where this is so, each separate stalk contains two traces, like the leaf, and the common peduncle has a corresponding number, which unite themselves into a vascular zone like that of the stem. To complete the picture we have another class of abnormalities in which the ovular stalks become definitely leaf-like. In such cases there is usually a stalk bearing a broad lamina with one or more ovules on its margin, the lamina being continuous with the collar of the ovule. Thus it seems clear that we are dealing with a reduced strobilus, which originally bore a number of megasporophylls of foliar nature, each with one ovule, though there is not enough evidence to show how they were arranged on the strobilar axis.

The ovule itself is very like that of *Cycas*. There is a thick integument, with the same three layers. There is one striking difference however: the integument in spite of its massive development has no vascular system. A concentric bundle from the axis splits into two below the ovule and the branches pass through the hard integument and spread out below the nucellus forming a mantle of short reticulate tracheids which covers the whole internal surface of the integument, as in some seeds of the Pteridosperms. The free apex of the nucellus breaks down into a pollen chamber and some of the mucilaginous material thus formed oozes out of the micropyle to form a pollination drop. The whole development of the megaspore, prothallus and archegonia also closely resembles that of *Cycas*, except that there is a definite ventral canal cell formed in the archegonium. This cell may later break down and its nucleus re-fuse with the oosphere nucleus, as may also happen in *Pinus*.

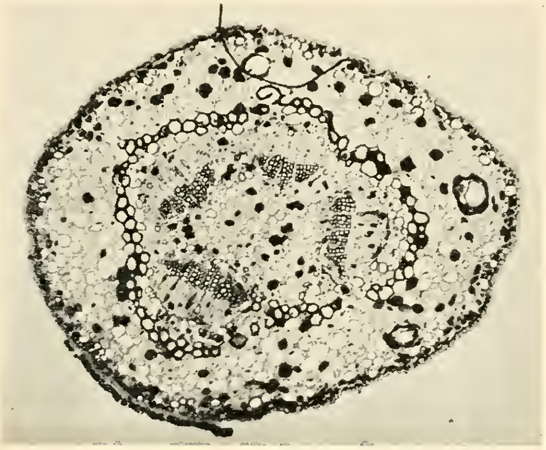

FIG. 744.—*Ginkgo biloba*. Transverse section of the ovuliferous shoot showing four bundles.

The young prothallus passes through a period of free nuclear divisions, usually eight or more, followed by centripetal growth of cells. The cells coming from opposite sides of the megaspore meet but do not join, so that a plane of cleavage is left down the middle of the prothallus. The whole prothallus is elliptical, not circular, in transverse section. The growing prothallus absorbs the spongy tissue of the nucellus around it and also most of the nucellar apex above it. It contains some chlorophyll, which might be regarded as a notably primitive feature, but is probably only a response to the penetration of light through the relatively thin stony layer of the integument, just as chlorophyll will develop in the pith of a translucent stem. There is a very thick megaspore wall and a delicate prothallus wall within it, which are quite distinct from each other.

Archegonia begin to develop even before the prothallus tissue is complete. Only two are formed, side by side, in the plane of the longest diameter of the prothallus. They are short and broad, quite different in shape from those of Conifers and Cycads (Fig. 745).

Instead of the archegonial chamber of *Cycas* a ring-shaped trough is formed, surrounding a central beak which supports the remains of the nucellus. It is called the **tent pole,** and a similar structure is prominent in some Pteridosperm seeds.

The ovuliferous axes begin to appear in April, at the same time as the male catkins. At first they grow very rapidly and pollination takes place about the beginning of May, when only the megaspore mother cell has been formed. Fertilization is delayed until late in September, *i.e.*, four months from pollination, as in *Cycas.*

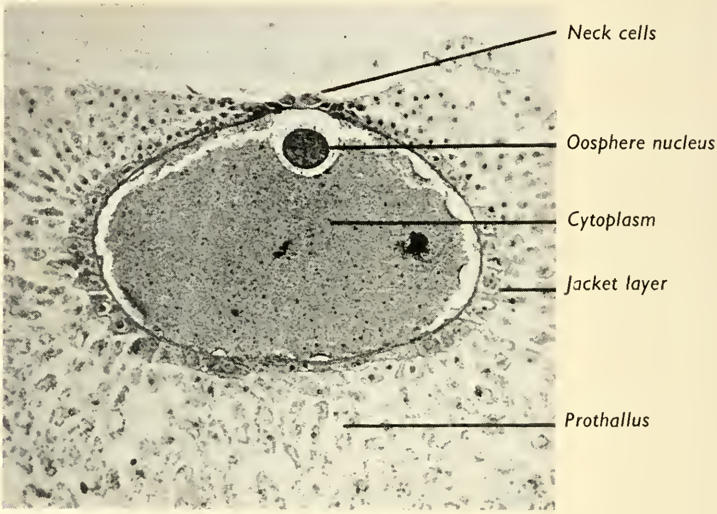

FIG. 745.—*Ginkgo biloba.* Longitudinal section through the apex of the female prothallus showing an archegonium.

The pollen grains in the pollen chamber soon begin to germinate. The extine does not cover the whole cell, and there is a thin portion covered only by the intine, which now protrudes and forms an haustorial tube, burrowing into the nucellus, as in *Cycas.* At the pollen grain end this tube is enlarged and almost bladder-like and it pushes the grain down through the floor of the pollen chamber, which disintegrates into the space above the archegonia.

Meanwhile the antheridial cell has divided into a stalk cell and a body cell, while the latter divides again, vertically, to form two cells, in each of which an antherozoid develops (Fig. 746). These are very like those of *Cycas*, but not quite so large (about 80μ as against 250μ), and they are more elongate, but they have the same spiral blepharoplast with hundreds of cilia. They are apparently liberated as in *Cycas*, but details are uncertain.

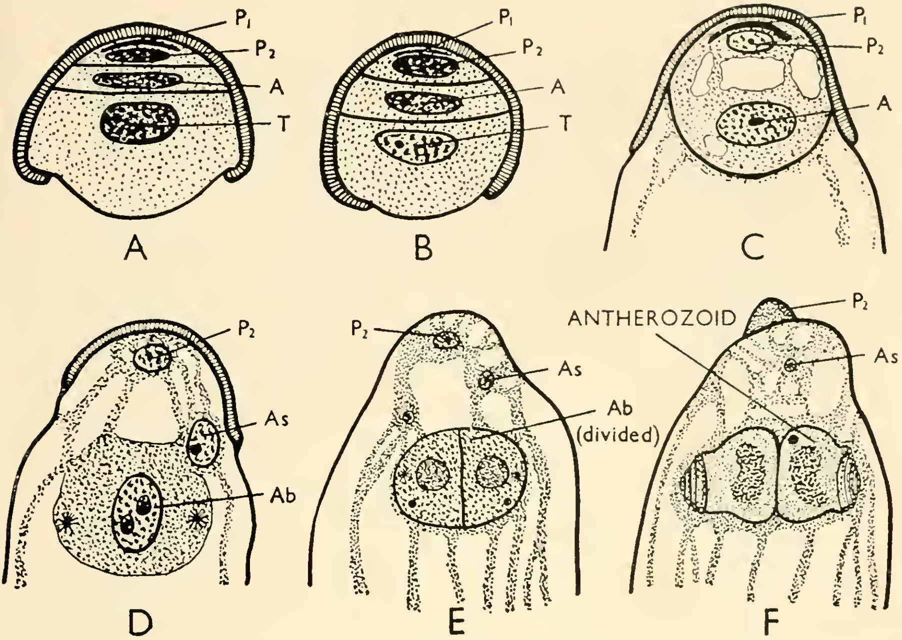

FIG. 746.—*Ginkgo biloba.* Development of the male gametophyte. A, Antheridial cell. Ab, Antheridial body cell. As, Antheridial stalk cell. P1 and P2, Prothallial cells. T, Tube cell. Note that the extine only partially covers the spore. (*After Hirase.*)

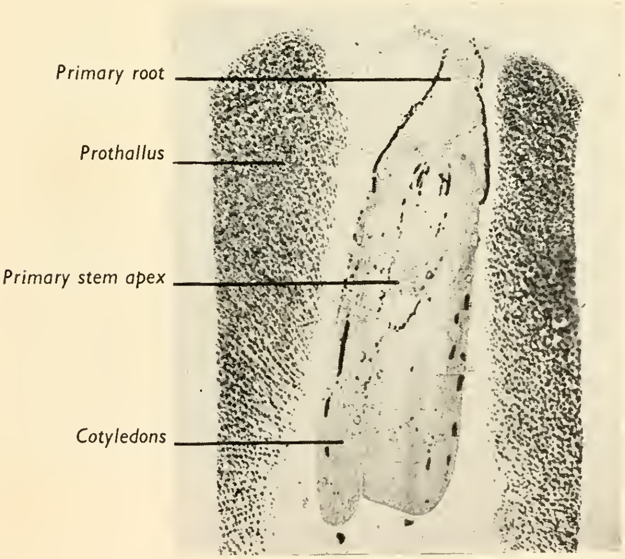

FIG. 747.—*Ginkgo biloba.* Longitudinal section through a mature embryo surrounded by prothallial endosperm. Note the unequal size of the two cotyledons.

EMBRYOGENY

Development begins with a period of free nuclear division, followed by wall formation, and the whole contents of the archegonium become cellular. This mass of undifferentiated cells is known as the **protocorm** and has a parallel in some Cryptogamic types such as *Lycopodium*. There is no special suspensor development but the cells in the neck region enlarge while those near the base become numerous and remain small. It is from these latter that the embryo develops. It is quite straight and dicotyledonous (Fig. 747), but there is a precocious formation of foliage leaves from the plumule and at germination there are usually five present.

The embryo lies embedded in the prothallial tissue which serves as endosperm. It is reported that the micropylar end of the protocorm grows out into the endosperm and may act as an haustorium, but this is uncertain.

In the interval between May and September the ovules often fall from the tree. Fertilization and embryo development then proceed while they are lying on the ground. This may perhaps account for the strange absence of embryos in the fossil seeds of Pteridosperms. If embryo formation were very much delayed and then proceeded continuously, with no resting phase, it is scarcely to be expected that we should find embryos in the seeds.

As the embryo matures the integument also enlarges and the outer flesh thickens, producing a mature " fruit " about an inch long (Fig. 748). The inner flesh becomes papery but the outer flesh is very mucilaginous and has an unpleasant smell. The " kernel," *i.e.*, the endosperm, is, however, edible.

The symmetry of the seed is slightly bilateral, corresponding to the oval section of the prothallus, and the longer diameter is marked by two prominent ridges on the hard testa. Seeds with three ridges sometimes occur, which strongly resemble the Medullosean fossil seed *Trigonocarpus*.

Usually only one of each pair of ovules develops to maturity, though exceptions are not infrequent.

GERMINATION

The two cotyledons are somewhat unequal : the larger is slightly notched at the apex but the smaller is cleft nearly into two. In each lobe there are single bundles which unite at the base of the cotyledon into a double bundle with mesarch structure. This is almost the only relic in *Ginkgo* of the mesarchy which marks the foliar bundles of *Cycas*. Its presence here supports the belief that seedling structure may retain ancient characters and shows that *Ginkgo* has departed further from the primitive Fern stock than have the Cycads, at least in some respects.

The cotyledons are hypogeal and remain persistently embedded in the nutritive endosperm. There is a primary tap root, and the young leaves are deeply bilobed (Fig. 749). A point of interest is that the young leaves during development are bent over at the apex and the margins are rolled in

FIG. 748.—*Ginkgo biloba*. Shoot bearing a mature ovule.

(*From a photograph by Mr E. Cahen.*)

towards the middle. Such inrolling suggests a relic of the circinate vernation of Ferns, traces of which, as we have seen, still linger in the Cycads.

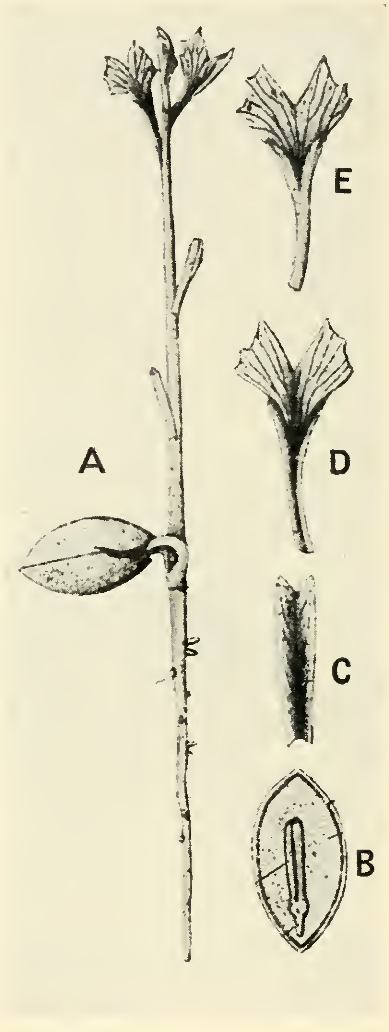

Fig. 749.—*Ginkgo biloba.* Seedling development. A, Seedling with cotyledons still embedded in the seed coat. B, Longitudinal section of the seed with straight embryo embedded in endosperm. C to E, Series of youngest leaves showing the development of the bilobed leaf. (*From Velenovsky, "Vergleichende Morphologie der Pflanzen."*)

A peculiarity of *Ginkgo* which suggests a relic of pinnation in the leaf is this ; the first epicotyledonary leaves are merely forked scales. The second pair have a bilobed lamina, at the base of which are two lateral prongs, representing the forked scales. These leaves therefore appear to have two normal and two reduced segments, one above the other.

RELATIONSHIPS

Ginkgo occupies such an isolated position that its relationships are uncertain. Mention has been made of the fossil genus *Baiera* (Permian to Jurassic), which was certainly a close relative. In it the following characters, which we have noted as abnormal in *Ginkgo*, are the rule ; namely, multilobed leaves, numerous ovules branching from one peduncle and numerous microsporangia on each sporophyll. Another genus, *Trichopitys* (Permian), may also belong here. It has forked leaves with narrow segments, and above, but not in, the leaf axils there are ovuliferous branches with numerous, apparently pinnate, sporophylls, each bearing a terminal ovule. Beyond the suggestion of relationship to these two genera we have little to guide us, but there can be little doubt that the family arose from an early Pteridosperm stock, probably before the Cycads, and has remained distinct ever since Palaeozoic times.

Gnetales

The Gnetales are usually included in the Gymnospermae on the ground that in them pollination is still an ovular function and that no style or stigma is present, as it is in all typical Angiosperms. The ovules are, however, enclosed within coverings additional to the true integument, and these are sometimes considered to be the equivalent of ovary walls.

A common character of the group is the prolongation of the apex of the integument into a long narrow tube with a flattened orifice, by means of which the pollen is collected. The organs producing the microspores resemble the stamens of Angiosperms, consisting of a short axis or stalk bearing a terminal group of more or less united microsporangia.

Once more we have to deal with a group of plants containing a small number of very distinctive and widely scattered forms, which have the appearance of being the remains of a formerly larger and more united order. Fossil remains of the group are, however, remarkably few and do not go back beyond the Tertiary period, so that we have little idea of their ancestry. The living forms are all highly specialized in structure and have departed so far from the primitive gymnospermic stock that they are probably of fairly recent appearance. Moreover they are predominantly plants of dry situations, and plants growing under such conditions are unlikely to be fossilized (Fig. 750).

They are so advanced in structure that in several respects they approach the Angiosperms. No direct relationship can, however, be considered possible. Whatever the ancestry of the Angiosperms may have been, it was at least not among the Gnetales. They are a parallel line of evolution and, so far as we can see, a blind alley, but not only are they morphologically striking in themselves, they also show us the summit of gymnospermic development from a cordaitalean ancestry.

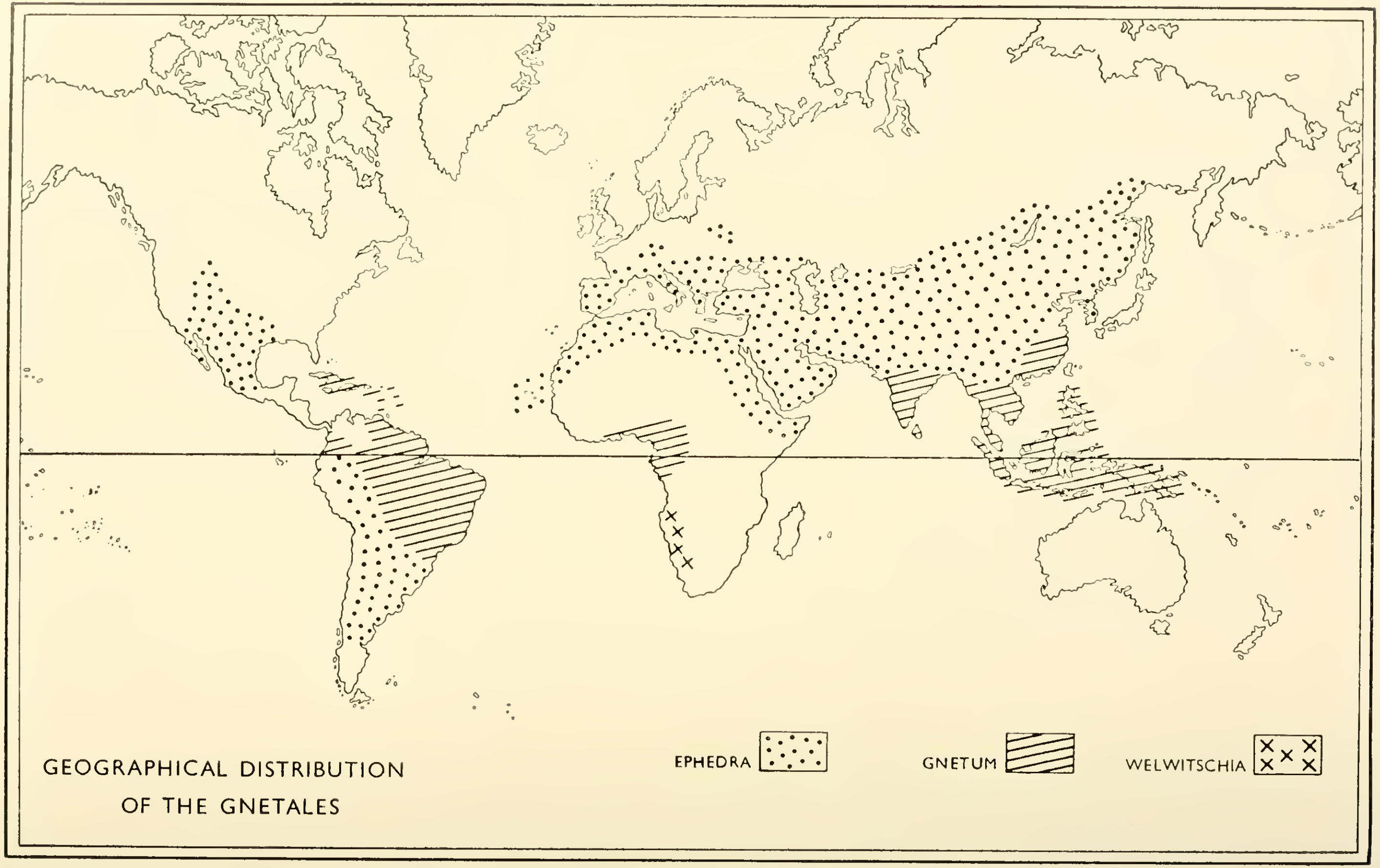

Fig. 750.—Geographical distribution of the Gnetales.

There are three living genera, sometimes classified as three distinct families, and with comparatively little in common except in the reproductive structures.

The genus *Ephedra* consists of shrubby, Broom-like plants with minute leaves. There are about thirty-five species, divided between the Old and the New Worlds. The species have mostly a restricted range and there is none common to both sides of the Atlantic. In Europe they range round the Mediterranean region and eastwards through Central Asia. In America they are confined to the south-western United States and Mexico, also along the Andes and across Argentina.

The genus *Gnetum* includes trees, shrubs or woody climbers, the latter form predominating. There are about thirty-four species scattered in a belt of the Tropics from the East Indies, through West Africa to the Amazon region, and they are invariably jungle plants. Their vegetative appearance is entirely Angiospermic, and their large net-veined leaves cannot be distinguished from those of Dicotyledons.

The genus *Welwitschia* comprises the most remarkable living plants. There is only one species, *W. mirabilis*, which is practically confined to the Namib desert region of South-West Africa. It also occurs farther north, growing in moist conditions and even under the shade of trees. The stem resembles an enormous woody carrot the top of which is concave and may reach 4 ft. in diameter. It is almost entirely buried in the sand and bears only two long strap-shaped leaves which persist throughout life.

It is obviously impossible to give a generalized account of so diverse a group, but one common feature, however, deserves comment. All three genera have compound male strobili, *i.e.*, the males, like the females, are inflorescences, not single flowers, and this distinguishes them from almost all other Gymnosperms.

In the face of such striking divergences between members of one systematic group it becomes necessary to consider in detail each genus separately. The same objection applies with even greater force in dealing with the Angiosperms, and from that point onwards our descriptions must be general and comparative rather than particular.

Ephedra

All the species of *Ephedra* are woody, some are climbers and a few are prostrate. Many spread by rhizomes from underground buds. The branches are green and slender and the leaves usually minute (Fig. 751). The whole aspect of the plant is xeromorphic and strongly recalls a *Cytisus*. The leaves are usually in opposite pairs, decussately arranged, and are joined (**connate**) to each other at their bases to form a small sheath. Leaves in threes and fours also occur, the latter rarely.

The branches come from axillary buds and are therefore in pairs or threes according to the species. The first branches often come from the axils of the cotyledons. Branching of the side shoots is confined to the lowest two or three nodes, and as these are very close together the effect is often that of a whorl of branches all seeming to come from the node of the parent stem. This adds to the density of the bush (Fig. 752).

The growth of the internodes is independent and is due to a pale-coloured meristematic zone at the base of each. At the end of the growing season the meristem in some species hardens into an abscission layer and the branches drop off, to be replaced next season by axillary shoots.* These species may be called deciduous, by analogy with trees which drop their leaves in winter. The apex of each branch is formed by a bud consisting of the first four or five undeveloped internodes, wrapped in the scale-like leaves.

FIG. 751.—*Ephedra nebrodense.* Shrubby habit of plant. Kew Gardens.

ANATOMY OF THE STEM

The surface of the stem is ribbed. There is a very thick epidermis, which is supported below the ribs by groups of fibre cells. Stomata, each sunk in a circular pit, occur in the furrows between the ribs. They open into a cortex which is differentiated into a loose, outer palisade layer and an inner spongy tissue, both containing chlorophyll and being responsible for all the effective photosynthesis carried on by the plant. An endodermis

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* A similar abscission occurs in the Poplar and the Oak and has been called **cladoptosis,** as the abscission of leaves is called **phylloptosis.**

surrounds the ring of vascular bundles, which are all collateral and endarch (Fig. 753). Large and small bundles are grouped into pairs or threes. Two small bundles form each leaf trace. These bundles each run a course through two internodes and then pass out in pairs into the leaves. There is thus a double leaf trace, in spite of the rudimentary character of the leaves, and we can hardly avoid concluding that this doubled trace is really an ancestral character, pointing backwards in time to the double trace of the Pteridosperms.

FIG. 752.—*Ephedra nebrodense.* Portion of a shoot to show the whorls of assimilatory branches. Note the general resemblance to the habit of *Equisetum.*

A cambium is present and older stems become greatly thickened by secondary growth (Fig. 754). Annual rings are formed in the secondary wood as growth proceeds, but *Ephedra* is not a very long-lived plant and half a century probably represents its maximum duration. Medullary rays in the young stems are uniseriate, but in older stems they become very broad and long, vertically, partly by their own growth and partly by fusion of neighbouring rays. Their cells are all lignified, so that the wood texture is very hard. The tracheids have single rows of scattered bordered pits, both on the radial and tangential walls. Alternating double rows also occur. Rims of Sanio and trabeculae across the tracheids are also present.

The outstanding feature of the whole stem histology is, however, the presence of **vessels**, resembling those in Angiosperms. These are formed most abundantly, and are individually largest, at the beginning of growth in the spring. They later decrease in size and in numbers and the autumn

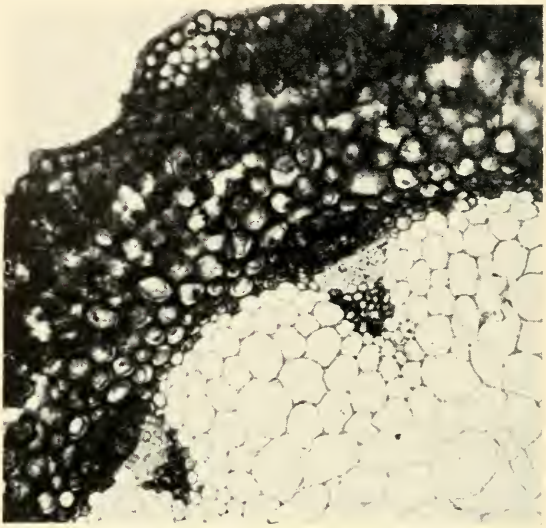


FIG. 753.—*Ephedra sp.* Transverse section of the stem showing the cortex containing chloroplasts and two of the primary vascular bundles at the margin of the large-celled pith.

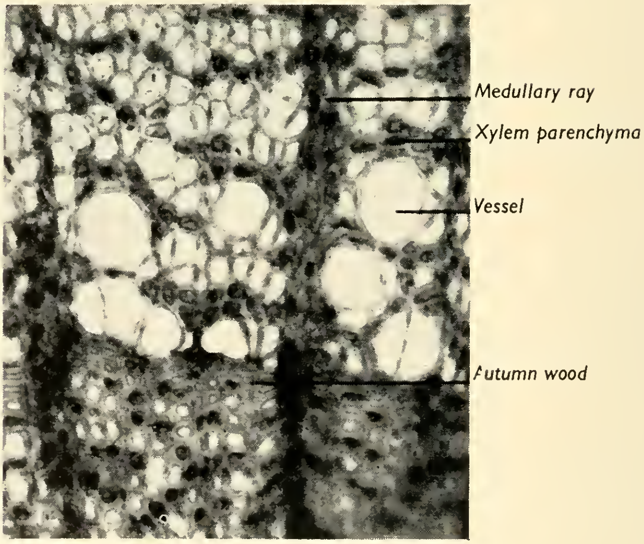


FIG. 754.—*Ephedra sp.* Transverse section through the secondary wood of the stem showing the large vessels and the boundary of an annual ring.

wood contains none at all. Each annual ring of wood is therefore marked by the limited distribution of the vessels in a narrow band, this constituting the type of wood structure called **ring porous**. The pits on the end walls of the vessel elements are at first ordinary bordered pits, but the border and the closing membrane are absorbed at an early stage of development, so that perforations are left which often become confluent into irregular apertures, leaving open connections between successive vessel elements. There is no complete absorption of the end walls, as happens in the higher Angiosperms, but parallels to this partial absorption can be found in many Angiosperms belonging to what we consider " lower " groups such as the Magnoliaceae.

At or near the nodes the pith cells become strongly lignified, forming transverse plates. It is in these regions that the winter abscission of young branches occurs.

There are no resin ducts, but cells with large stellate crystals of Calcium oxalate are abundant.

In the third or fourth year a phellogen arises just outside the phloem and the periderm formed from it displaces all the outer tissues.

The meristems of *Ephedra* are poorly differentiated into distinguishable layers. In the stem apex even the surface layer is not clearly separated from the central mass of meristem cells, which differentiates directly into the respective permanent tissues.

REPRODUCTION.

Both male and female reproductive organs are borne on small strobili, the scales of which are arranged in decussate pairs, each pair being concrescent at the base. These strobili are normally axillary on young shoots, either singly or in small sessile groups, which really represent suppressed branches.

There are certain problems of morphological interpretation regarding these strobili which will be discussed briefly later.

Ephedra is normally dioecious, but monoecious plants and even hermaphrodite flowers are known. Bisporangiate strobili produce stamens at the base and ovules above, as in the similar cases in Coniferales.

THE MALE STROBILUS.

Each male strobilus stands in the axil of a leaf and each has a short axis bearing a number of rather thick and closely set scales or **bracts,** arranged decussately in pairs (Figs. 755 and 756). The number of pairs varies between two and twelve. In the axil of each bract stands a single male flower (Fig. 763), which consists of a perianth of two scales, from between which arises a **stamen,** consisting of a stalk, at the top of which is a variable number of anthers. These are normally sessile, but in species where the anthers have individual filaments they make the stalk appear to branch apically.

The nature of the stalk or **antherophore** is uncertain. It may be either an upgrowth of the flower base or formed by a fusion of anther filaments.

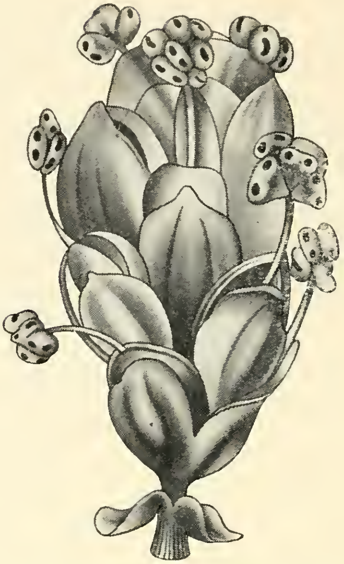


FIG. 755.—*Ephedra fragilis.* Male strobilus. (*After Stapf.*)

FIG. 756.—*Ephedra sp.* Branch bearing male strobili with exserted stamens.

Most probably it varies, being partly of one nature or the other in different species. Each anther is supplied with one vascular bundle, derived from the branching of the pair of bundles which enter the stalk at its base, the branches running parallel upwards to the anthers.

The anthers themselves have either two or three lobes, each lobe opening by an apical slit. The pollen grains are elliptical.

The Female Strobilus.

The female strobili are distributed in the axils of the leaves on the young shoots in the same way as the males, and they are very similar in structure though rather shorter, with only two to four pairs of bracts (Fig. 757). Each strobilus ends in a group of female flowers, one, two or three in number, each consisting of a nucellus with two envelopes. The arrangement recalls that in the Taxales, and a similar difficulty of morphological interpretation meets us here. The inner envelope is formed of two segments and contains two bundles, while the outer envelope is formed of four segments and has four bundles. Comparison with the flowers of *Welwitschia* suggests that the nucellus is terminal on a suppressed branchlet of the strobilus, that the inner envelope is a true ovular integument, and that the outer envelope is a perianth, the whole structure being axillary to one of the bracts of the uppermost pair.

The upper half of the nucellus is free from the inner integument, and the latter is prolonged into a thin-walled micropylar tube which is sometimes spirally twisted and opens at its tip into a tongue-like extension. Here the pollination drop is extruded, by means of which pollen is drawn down into the micropylar tube. The perianth fits closely over the integument and becomes woody or fleshy, forming the outer coat of the developed seed.

Fig. 757.—*Ephedra intermedia.* Female strobilus with two female flowers. (*After Stapf.*)

The bracts of the strobilus are in some species dry and winged, in others fleshy and sometimes brightly coloured, corresponding to the means of dispersal, either by wind or by animals, which is characteristic of the particular species.

The Male Gametophyte.

The divisions of the nuclei in the microspore follow the *Pinus* plan, a small but positive sign of linkage with the Conifers. Two prothallial cells are formed, together with an antheridial stalk cell and a body cell, the latter of which divides to form two male nuclei. Lastly there is a spore-cell nucleus, which later becomes the tube nucleus (Fig. 758). This differentiation is completed before the shedding of the pollen, and the disappearance of the two prothallial cells follows almost immediately.

On arrival at the ovule, germination of the pollen grains is very rapid. The extine is thrown off and a germination tube appears at once, into which pass the tube nucleus and the two male nuclei, accompanied by the nucleus of the stalk cell.

Fertilization occurs less than twelve hours from pollination, a remarkable contrast to the prolonged delay characteristic of most Gymnosperms. The pollen tube penetrates between the neck cells of the archegonium and the two male nuclei pass directly into the oosphere.

The Female Gametophyte.

The thin inner integument grows out into a long pollen-catching micropylar tube, which becomes twice as long as the perianth. The apex of the nucellus develops a pollen chamber, the bottom of which goes right through to the apex of the prothallus (Fig. 759). The pollen thus actually reaches the female prothallus itself, a feature in which this type of ovule is unique. The prothallus develops from the lowest of a row of four megaspores. There is first a period of free nuclear division, which reaches at least the 256-nuclear stage before cell walls are formed, but the details are not known. The mature prothallus is elongate and has two clearly distinguishable regions. The micropylar region, usually with two archegonia, is formed of elongated, thin-walled cells, with a central strand of almost empty cells running downwards to the lower, antipodal, region of the prothallus. The latter region is composed of small, regular cells with much denser contents, especially in the central cells, which are evidently a nutritive tissue. Two outer layers, called the **haustorial layers,** apparently act as absorbers of material from the nucellus. The archegonia are also elongated and have a jacket layer of cells which is not very well defined. The archegonia develop from superficial cells of the prothallus and have at first a neck with only three tiers of cells, but, by the upgrowth of the prothallus apex, the number of neck cells becomes so great that eight or more tiers of cells may overlie the top of the oosphere, which is thus more deeply sunken in the prothallus than in any other living plant. This upgrowth of the prothallus should be noted in comparison with the formation of much more pronounced upgrowths in *Welwitschia.*

In the oosphere there is a large nucleus, with a dense plasmatic sphere around it, and a large ventral canal nucleus but no ventral canal cell.

Fertilization.

Both of the male nuclei are released into the archegonium, but only the first unites with the female nucleus. The second male nucleus and the

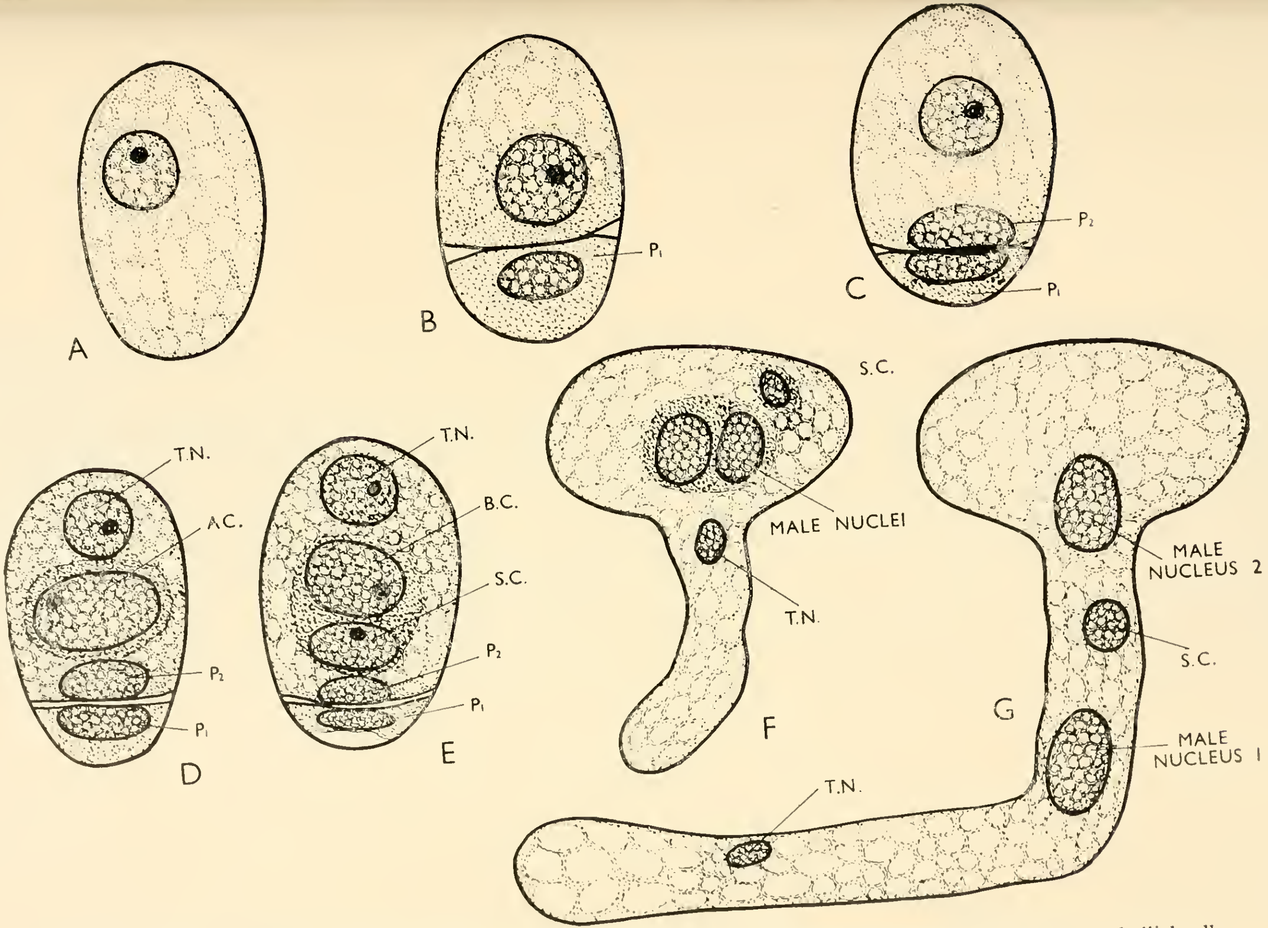


FIG. 758.—*Ephedra trifurca*. Successive stages in the development of the male gametophyte. P1 and P2, Prothallial cells. TN, Tube nucleus. AC, Antheridial cell. BC, Body cell. SC, Stalk cell. (*After Land.*)

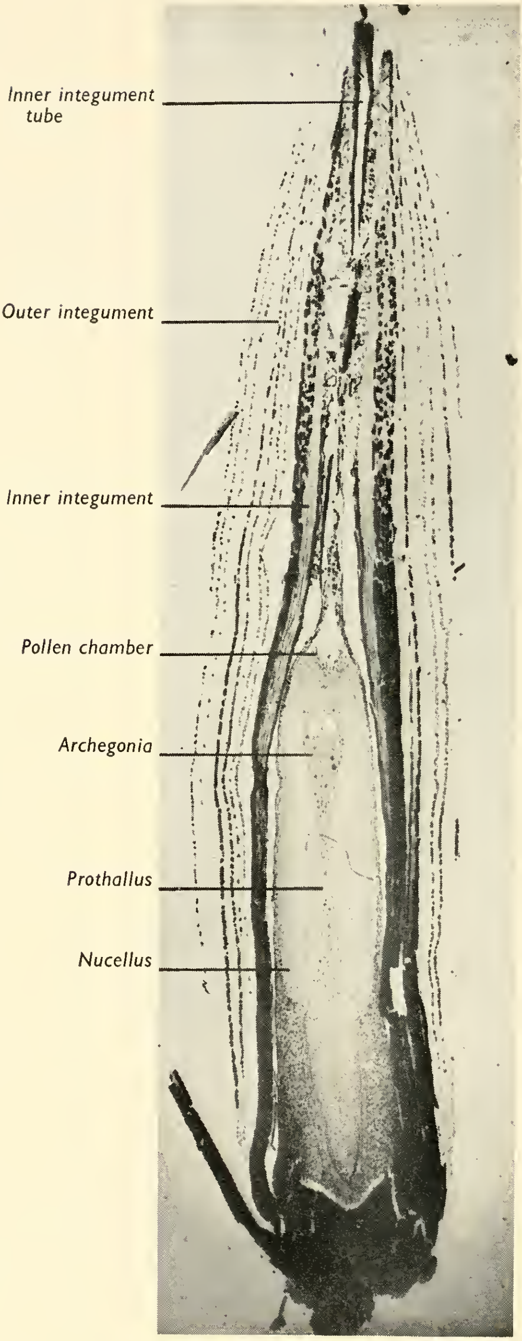


FIG. 759. — *Ephedra sp.* Vertical section through an ovule at the fertilization stage.

ventral canal nucleus seem to break up and form the nuclei for a number of small ephemeral cells at the top of the oosphere, but the details are uncertain. This tissue is regarded as a physiological "endosperm," for it is soon absorbed by the growing embryo. Meanwhile the cells of the jacket layer fuse with the oosphere, and their large nuclei and their cytoplasm mingle with the contents of the oosphere. The fertilized oospore nucleus divides into eight, of which from three to five may give rise to embryos. Those which begin development commence by surrounding themselves with cell walls.

Embryogeny.

Each primary embryonic cell begins development by the division of its nucleus into two of unequal size. A tubular outgrowth appears into which the larger nucleus passes and moves down to the tip of the tube, and behind it a cross wall is formed. This terminal cell divides and becomes a pro-embryo. The remainder of the tube forms the suspensor, which elongates and pushes the young embryo down into the nutritive tissue at the base of the prothallus. The basal cells of the pro-embryo likewise elongate, though not greatly, and form a secondary suspensor, which is not clearly distinguishable from the root cap of the embryo proper. Only one embryo usually matures.

While the embryo is developing the apex of the prothallus becomes meristematic and builds a layer of protective tissue which closes the base of the pollen chamber and prevents the suspensor from being pushed upwards out of the prothallus.

Germination.

The seed has no obligatory resting period and may germinate immediately. The two cotyledons are linear and grow steadily until they are several centimetres long. As the plumular leaves are reduced to scales from the beginning, the cotyledons are responsible for all photosynthesis in the early stages of growth. Each cotyledon contains two parallel bundles which unite basipetaly and pass into a diarch root system.

Gnetum

The genus *Gnetum* is superficially very distinct from *Ephedra* but has many points of coincidence in structure. It is distributed all over the Tropics, and the thirty-four species are all lanky trees or climbers.

Vegetatively the most striking feature is the dicotyledonous type of foliage, with net-venation, which is quite indistinguishable from that of an Angiosperm (Fig. 760). Anatomically the stem is characterized by the presence of wood vessels (Fig. 761) and by the peculiarity, in the climbing species at least, of forming successive concentric zones of vascular bundles, as in the stems of some Cycads.

The perforations of the vessels differ from those of *Ephedra* in consisting of one large aperture only (Fig. 762). This is more like the typical form of vessel in the Angiosperms, but it is produced by the confluence of a number of bordered pits as in *Ephedra*, and thus is radically different in origin from the vessel pores of the Angiosperms, in spite of a superficial resemblance.

A further distinction from the structure of Angiosperms is found in the phloem. The sieve tubes and their companion cells originate from separate cells in two different layers of the cambium instead of, as in the higher group, from the subdivision of single cells.

FIG. 760.—*Gnetum gnemon*. A branch showing dichasial branching and leaves of the dicotyledonous type. Much reduced.

In the branching of *Gnetum* there is commonly more than one axillary shoot from each leaf axil of the primary stem, and these side shoots are differentiated into indeterminate or long shoots and determinate or short shoots, the latter bearing one to eight pairs of decussately set leaves. The leaves on the long shoots may be either normal foliage leaves or, in the climbing type, may be reduced to scales.

REPRODUCTION.

Most of the species are normally dioecious, but reduced, functionless, female inflorescences may occur on male plants (cf. *Welwitschia*). Both male and female inflorescences are strobili, several centimetres long, arising in the leaf axils. At the base stands a pair of bracts from between which rises the main strobilus, and lateral strobili also grow from the axils of these basal bracts. All of these may branch again, but unbranched strobili are characteristic of some species.

The successive pairs of bracts on the strobilus itself are each united into a cup surrounding the axis. In the axils of these appear, in the male, two to five whorls of male flowers, and, in the female, a single whorl of four to ten female flowers. In both sexes the flowers are surrounded by fine hairs.

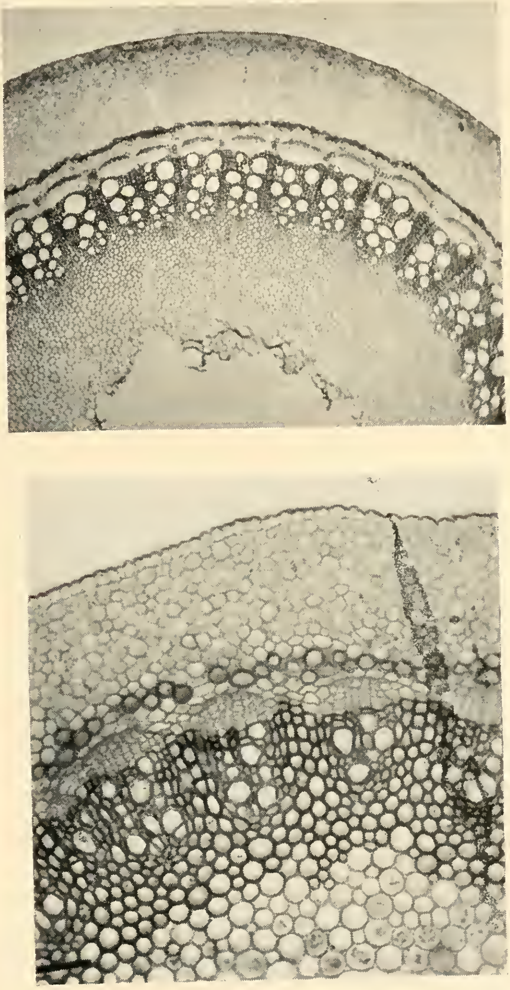


Fig. 761.—*Gnetum gnemon.* Transverse section of the stem at the beginning of secondary thickening, at two different magnifications, showing the well-marked pericycle and the large vessels in the wood.

The Male Flower.

Each male flower is surrounded by a perianth, formed of two segments which early become fused into a tube, from within which springs a filamentous stalk bearing one or two simple anthers, each dehiscing by an apical slit. The construction is thus very similar to that of the stamen of *Ephedra* (Fig. 763).

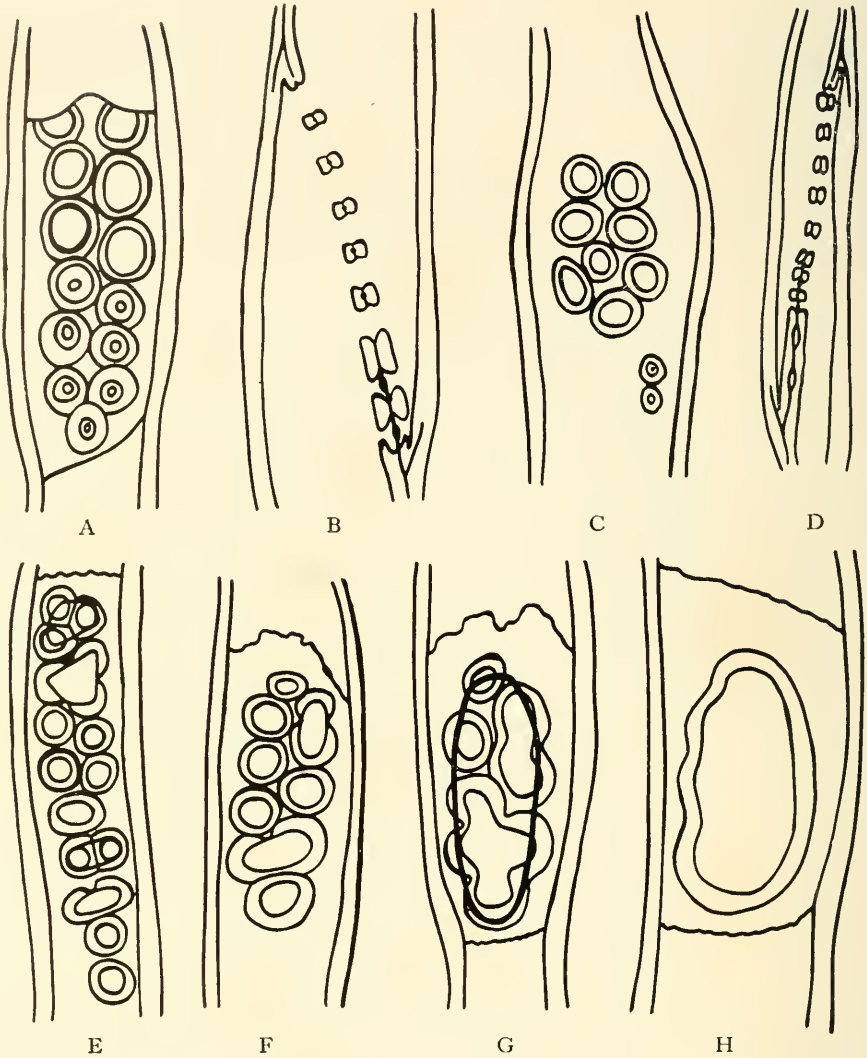
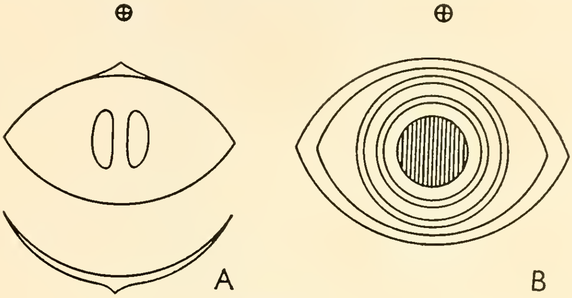


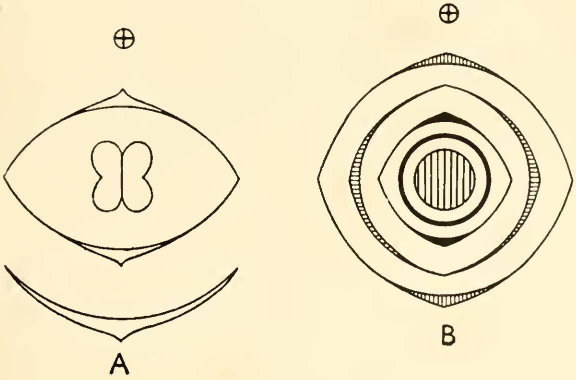
Fig. 762.—Comparison of vessel perforations in *Ephedra* and *Gnetum*. A and B, *Ephedra monostachya*, showing the relationship between vessel perforations and bordered pits. Vessel plate in surface view and section. C and D, *Gnetum gnemon*. Vessel plate from the root of a seedling showing correspondence with the *Ephedra* type. E to H, *Gnetum moluccense*. Series of stages from the node of a seedling showing transition from E, *Ephedra* type, to H, *Gnetum* type. (*After Thompson.*)

The Female Flower.

The female flower is simply an ovule, consisting of a nucellus (a megasporangium) surrounded by three envelopes (Fig. 763). The inner is presumably an integument, comparable to that in other Gymnosperms, except that, as in *Ephedra*, it elongates into a micropylar tube. The morphological nature of the two outer coverings has been much discussed without any final result. The use of undefined terms such as "perianth," "ovary" and "cupule" really explains nothing. The principal fact is that they arise in acropetal succession as outgrowths of the base of the ovule itself and so cannot be regarded as modified bracts subtending the ovule. Both appear to arise from paired primordia, decussately placed, which fuse together at a very early stage. One or perhaps both may be equated to the paired perianth scales of the male flower, both here and in *Ephedra*, but the complete interpretation of the ovular coverings, not only in Gnetales but throughout the Gymnosperms, is not yet known.



Ephedra



Gnetum

FIG. 763 —Comparison of the floral diagrams of *Ephedra* and *Gnetum*. A, Male flowers. B, Female flowers. (*After Eichler*.)

The outer covering is fleshy, the middle covering is sclerotic but has a thick parenchymatous mantle round its upper end. The inner covering is prolonged into a long tubular beak, which projects through the micropyle beyond the outer coverings. This tube has two whorls of hairs, one directed upwards and another, lower down, directed downwards and engaging with the apex of the middle covering. The proliferation of the lining cells of the tube occludes its internal passage, and subsequent growth of the middle covering breaks the tube at the level of the lower whorl and lifts it clear of its basal portion, where it remains in the mature seed as a stopper, closing the micropyle.

The outer covering becomes finally orange red in colour, and the middle covering hard and sclerotic with a ridged surface (Fig. 764).

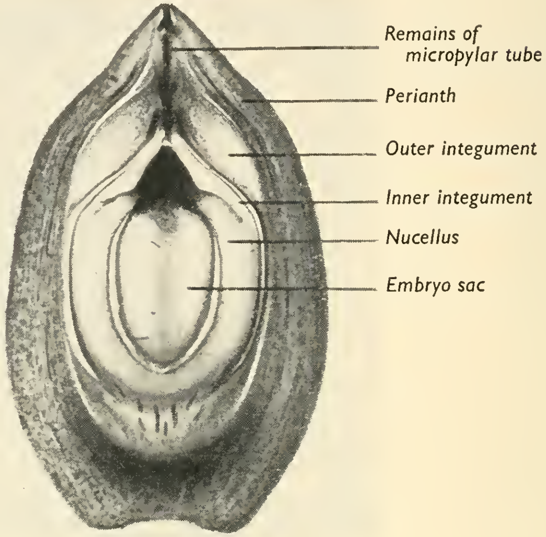


Fig. 764.—*Gnetum sp.* Longitudinal section through a mature ovule.

The Male Gametophyte.

The male gametophyte is incompletely known. The ripe pollen grain contains three nuclei, one vegetative, and comparable perhaps to the tube-nucleus in other types, the other two being gametic nuclei which enter the embryo sac. There do not seem to be any prothallial cells, but the first nucleus divides into two, one of which again divides and organizes stalk and body cells. The latter divides to form the two gametic nuclei (Fig. 765).

The Female Gametophyte.

The female gametophyte appears to differ markedly in different species. In the incompletely investigated but apparently primitive *G. ule* there seems to be a considerable development of female prothallial cells, occupying about two-thirds of the megaspore, the upper third being filled with a loose collection of tubular, multinucleate cells, which may be parthenogenetic embryos (no pollen tubes having been seen) or perhaps incipient prothallial tubes like those found in *Welwitschia.* In *G. gnemon*, which is better known, fertilization occurs in the free-nucleate stage of megaspore development. A prothallial tissue develops at the lower (antipodal) end of the megaspore, the cells of which are frequently multinucleate. Below the prothallus, a so-called " pavement tissue " of nutritive cells develops in the nucellus. The cells of this tissue form radiating rows and develop while the prothallus is still in an early free-nuclear stage (Fig. 766).

The outstanding fact is that no archegonia are formed and that apparently any of the nuclei of the embryo sac may be fertilized. Several pollen tubes may enter each embryo sac, and each of the two male gametic nuclei unites with a female nucleus (double fertilization) so that many zygote nuclei are produced, which enlarge and begin embryo development. Each surrounds itself with a cell wall and may unite with the tip of the pollen tube (cf. *Welwitschia*) or may remain free and eventually develop a tubular suspensor which pushes the embryo down into the antipodal end of the embryo sac. Some unfertilized female nuclei now divide to produce a prothallial tissue, while others disappear (Fig. 767). This tardy development of endosperm is, however, so vigorous that it invades and destroys the nucellus, only leaving an apical residue below the micropyle. At this stage the seed is shed and the further development of the embryo takes place on the ground, but its details are unknown.

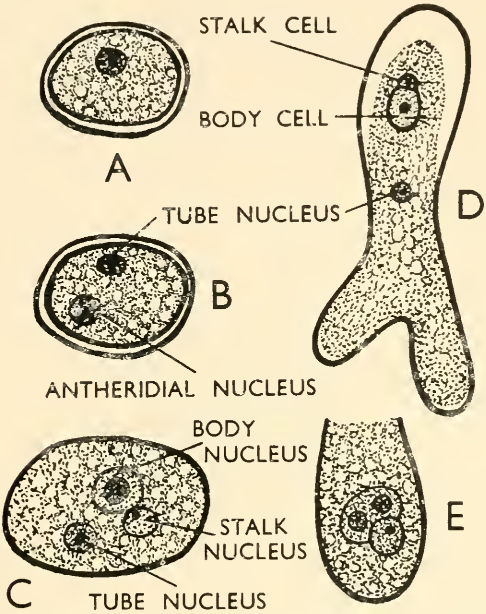


FIG. 765.—*Gnetum gnemon.* Development of the male gametophyte. A, Microspore. B, First division. C, Division of antheridial nucleus. D, Organization of antheridial stalk and body cells. E, Division of body cell to form male gametes. (*After Thompson.*)

Welwitschia mirabilis

The third genus of Gnetales is in many respects one of the strangest plants in the world. There is only one species, *Welwitschia mirabilis*, which is limited in its distribution to South West Africa (Fig. 768).

The habit of the plant may be likened to an enormous woody carrot, the top of which may be as much as 4 ft. across, though 2 ft. is the more normal mature size. It rises about 18 in. above the ground and tapers sharply downwards into a tap root which descends to unknown depths in the sandy soil. Across the top there is a deep furrow, running transversely to the leaves.

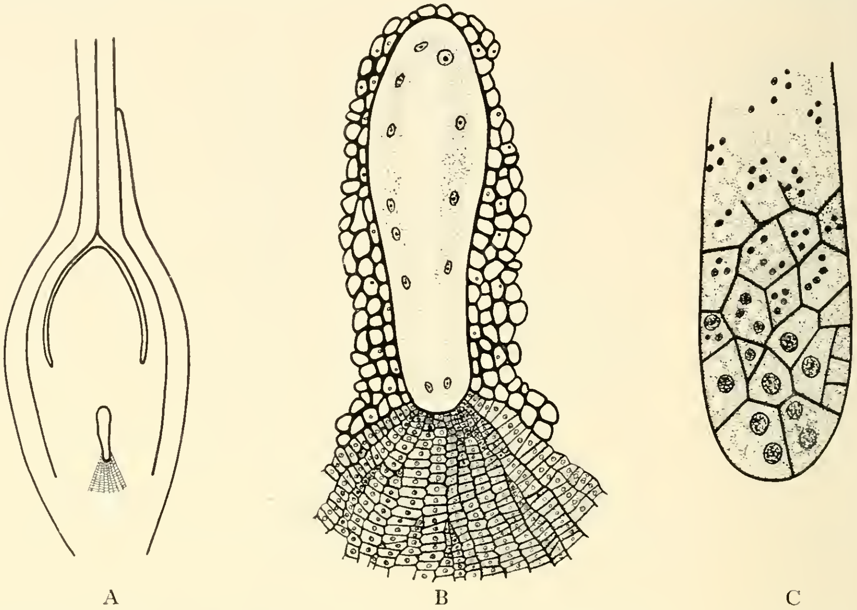


Fig. 766.—*Gnetum gnemon.* Development of female gametophyte. A, Longitudinal section of young ovule showing the deep-seated position of the embryo sac. B, Embryo sac with parietal nuclei and well-developed nutritive " pavement " tissue in the nucellus below the embryo sac. C, Mature embryo sac showing prothallial tissue formed at the antipodal end. (A *and* B *after Coulter*, C *after Thompson*.)

There are only two leaves, enormous leathery structures, like green straps, which lie on the ground and are usually more or less split into ribbons. They are about 6 ft. long in old specimens and about 1 ft. across. They arise from a pair of grooves, one on each side of the crown, which extend nearly round its circumference, and they continue to grow from a basal meristem during the whole life of the plant, which may last for a century.

The plant is invariably dioecious, though it has been recorded that young plants which have germinated close together may become so fused in growth as to be mistaken for a single plant, which may sometimes give rise to an appearance of bisexuality.

The inflorescences are male and female strobili, borne on branching stalks, arising from the rim of the crown, just above the leaf grooves.

Seedlings have often been raised in cultivation, and their development sheds light on the strange morphology of the adult plant. Germination is epigeal, the two cotyledons being withdrawn from the seed and turned up into the light. There is a short hypocotyl and a primary tap root. The seed contains nutritive endosperm and there is a lateral outgrowth of the hypocotyl, the foot, which remains inside the seed coat and acts as an absorber of nutriment from the endosperm. This recalls the similar embryonic structure in many Pteridophyta, though there is probably no direct relationship involved. The hypocotyl soon thickens into a small tuber and the stem apex produces two leaves, at right angles to the cotyledons, which, like the cotyledons, are at first erect. By the end of the first year all four have become horizontal. After two or three years the cotyledons drop off, but the two leaves remain permanently (Fig. 769). The growing point of the stem aborts and no further growth in length takes place. At a very early stage two little

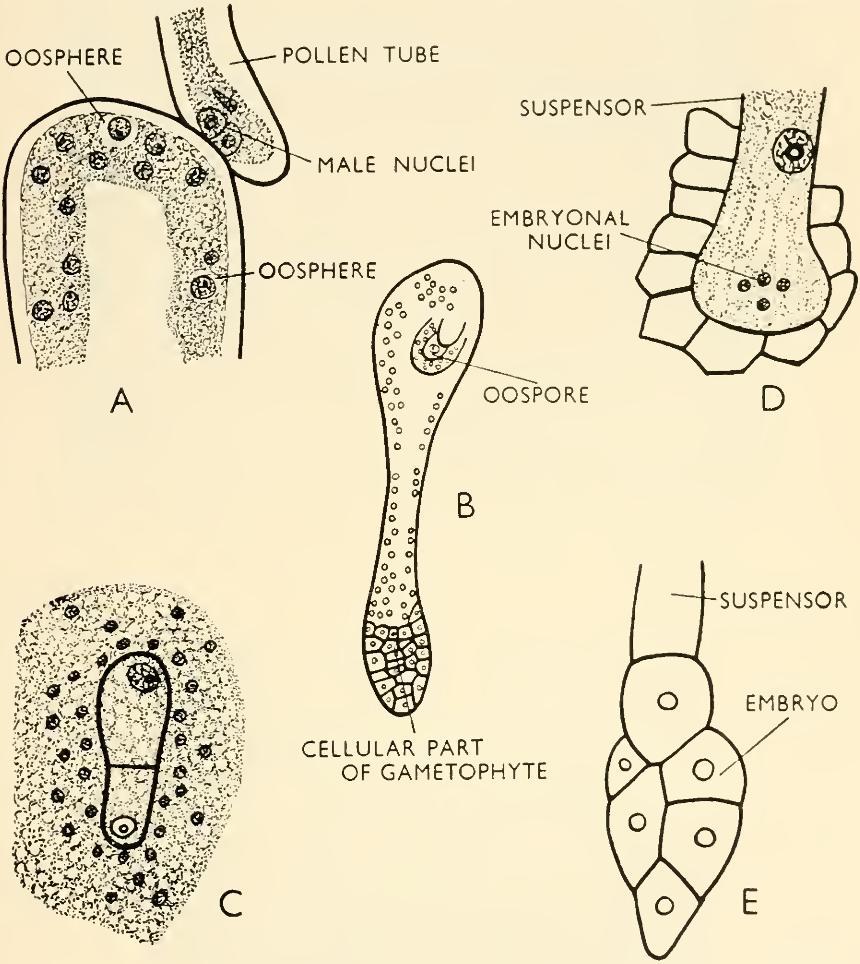


FIG. 767.—*Gnetum gnemon*. Fertilization and development of the embryo. A, Differentiation of the oosphere nuclei in the embryo sac. B, Embryo sac after fertilization. C, First division of the oospore to form the suspensor. D, Lower end of elongated suspensor showing primary embryonal nuclei. E, Early embryo development. (*After Thompson.*)

conical swellings appear on each side of the apex, at the base of the cotyledons. They are probably arrested axillary buds, but they become hard and scaly and spread until they cover the stem apex, which disappears under their united bodies. Meanwhile the axis is broadening by intercalary growth, and

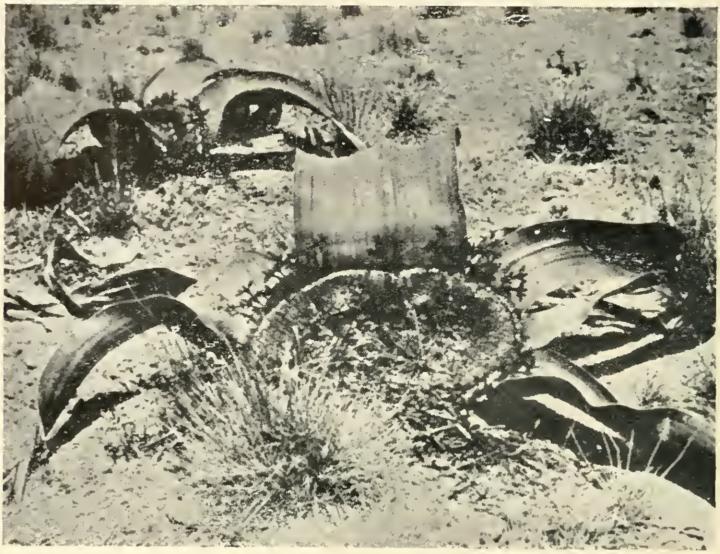


Fig. 768.—*Welwitschia mirabilis.* Old plants growing in Namib Desert in South West Africa showing reproductive strobili arising around the margin of the stem and longitudinal splitting of the old leaves.

(*Photograph supplied by the University of Coimbra, Portugal.*)

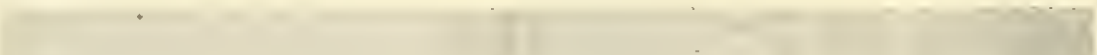


Fig. 769.—*Welwitschia mirabilis.* Young plant showing the two leaves which persist throughout the life of the plant and the tuberous stem.

a ridge appears below each leaf base, developing until it encircles the stem. A corresponding ridge arises above each leaf base, which is thus enclosed in a groove between the upper and lower ridges. The upper ridge increases in height and forms the rim of a saucer-shaped depression which includes the central part of the crown. As the crown grows broader the ridges, at first continuous, split along a line between the leaf bases and the crown becomes more or less two-lobed, with a V-shaped depression along the line of the split.

The upper ridge of the leaf-groove bears the branched inflorescences, which it continues to produce for several years. When it is exhausted it is succeeded by a series of new ridges formed outside it, one after another in centrifugal order, each bearing inflorescences for a time and then being superseded. The older ridges nearer the centre soon lose their identity in the thick growth of rough periderm which covers all the surface. These ridges arise at the leaf bases and correspond morphologically to branches or branch bases, which never develop vegetatively, but bear only the temporary reproductive shoots.

ANATOMY OF THE STEM.

The internal anatomy of *Welwitschia*, while not so peculiar as its external form, displays a number of interesting features.

In the young stem the bundles form a ring, but in the old stem the vascular tissue forms a cup-shaped mass extending from one leaf groove to the other. From this mass some bundles descend to the root and others ascend from its edges to the reproductive shoots. Everywhere are groups of sclereids, like those in the leaf, in such quantity that they make the whole tissue at first solid, but later it becomes spongy as the thin-walled tissue between them dies away, leaving the sclereids interlocking.

The individual bundles are of the dicotyledonous type, very long and narrow in the radial direction, like those of *Cycas*. Old plants show successive concentric zones of bundles, another cycadean character, also shared by some species of *Gnetum*.

The xylem consists of spiral, reticulate and pitted tracheids, the latter usually uniseriate. Vessels are also present, with incomplete perforations consisting of one or two simple irregular pits. The phloem is gymnospermic in type and has no companion cells.

Two crescentic groups of bundles pass upwards to the leaf bases. The ridges below and above each leaf base are supplied by very much flattened rings of bundles. Those in the upper ridge are said to originate from those supplying the lower ridge, passing upwards between the leaf trace bundles in their course from below to above the leaf base. The ridge bundles and those of the cotyledonary " buds " are said to end blindly downwards and are not attached to the main vascular system.

ANATOMY OF THE ROOT.

The primary root is diarch, and secondary thickening is more or less normal as far as is known, except that successive concentric zones of new bundles are formed, which become more definitely circular in arrangement with increasing age. These accessory bundles continue upwards into the hypocotyl and are distributed among the bundles which supply the ridges. This later development of bundle connections in all directions makes the anatomy of the mature plant an inextricable tangle of vascular tissue, continually added to by the ground tissue, which remains meristematic as long as it is alive.

ANATOMY OF THE LEAF.

The leaf has parallel venation, like a Monocotyledon, but with side branches which end blindly in the mesophyll as in a Dicotyledon. Each major bundle is enveloped in a transfusion tissue of tracheid-like cells and has a cambium which increases the bundle tissues by secondary growth (Fig. 770). Around each bundle are also numerous thick-walled fibre cells. The bundles are embedded in a thin-walled parenchyma, which is probably a water storage tissue. There is a well-marked palisade on both sides of the leaf, the epidermis is very thickly cuticularized and the stomata, in parallel rows, are deeply sunken (Fig. 771). Everywhere in the soft tissues are large numbers of lignified sclereids of multifarious shapes, in the walls of which are embedded numberless crystals of Calcium oxalate.

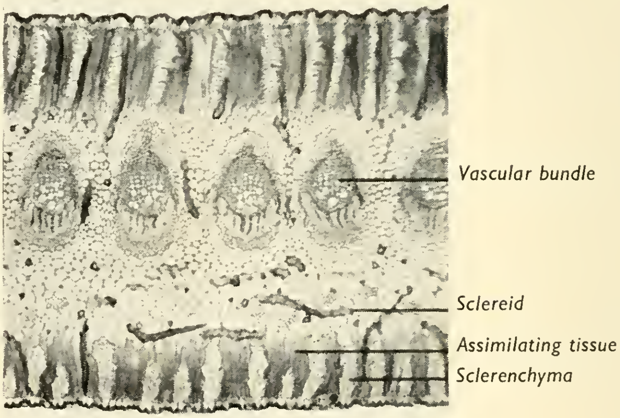


FIG. 770.—*Welwitschia mirabilis.* Transverse section of the leaf showing the row of large parallel vascular bundles.

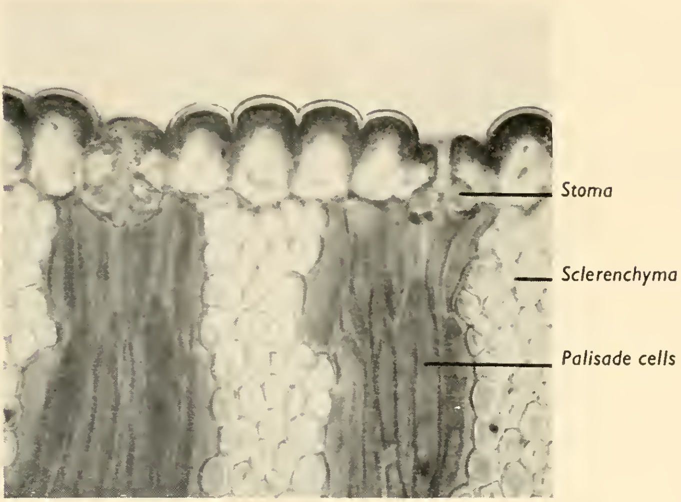


FIG. 771.—*Welwitschia mirabilis.* A portion of a transverse section of a leaf showing the sunken stomata and alternating bands of sclerenchyma and palisade cells.

THE INFLORESCENCES.

The branched inflorescences arise from oval depressions in the surface of the ridges, normally from the ridge above the leaf base, though the lower one also sometimes bears them. They are formed regularly every year and drop off after functioning, leaving a row of scars on the ridge. Each ridge apparently remains fertile for several years before being replaced by another, as described above.

Each inflorescence axis contains two irregular rings of vascular bundles, from the inner of which are supplied the bracts and branches. Below each node the bundles form irregular, convoluted groups, some with inverted orientation, which recalls the structure of the stem in certain fossil Medullosae.

The male axes branch dichasially two or three times, each pair of branches being subtended by a pair of connate bracts. The ultimate branches are the strobili, which are sessile and arranged in groups of three, a middle, terminal one with one at each side, each group being also subtended at the base by a pair of connate bracts. The strobili are bright red when ripe and form a striking contrast to their green stalks (Fig. 772).

THE MALE STROBILUS.

Each male strobilus is about 2 to 3 cm. long and rather slender. On its central axis are borne four rows of closely overlapping bracts, in decussate, connate pairs, the whole arrangement being geometrically regular (Fig. 773). In the axil of each bract, except a few basal ones, stands a single flower

FIG. 772.—*Welwitschia mirabilis.* Branching axis bearing male strobili.

(Fig. 774), furnished with two pairs of decussate, perianth scales, surrounding six trilocular stamens joined in a ring. The outstanding feature is the presence, in the centre of each male flower, of an abortive ovule, the

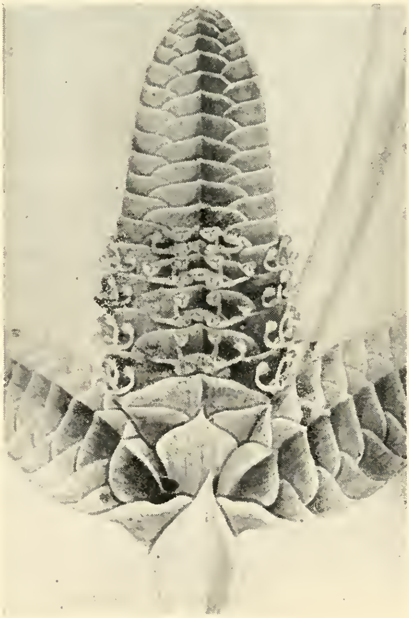


FIG. 773.—*Welwitschiamirabilis.* Group of three male strobili showing expanded male flowers and subtending bracts.
(*From Church, " Phil. Trans. Roy. Soc.,"* B, 205, *by permission of the Royal Society.*)

integument of which extends in the form of a tube as high as the stamens (Fig. 775). It is usually twisted and expanded at the top into a conspicuous disc, like a stigma. This ovule never matures, and its integumental tube is, moreover, quite different from that of the functional ovules.

It is not, however, quite functionless, for the nucellus secretes a sugary fluid which exudes on to the " stigma." This is similar to the drop-mechanism of pollination in the female flower, but in this case it presumably acts simply as an attraction which draws insect visitors to the male flower.

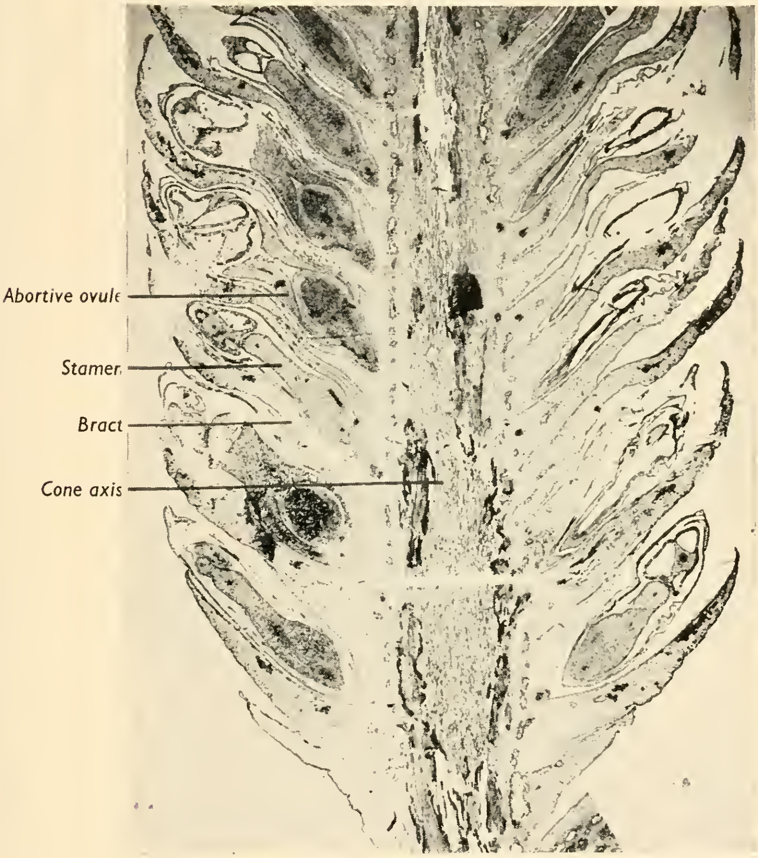


FIG. 774.—*Welwitschia mirabilis.* Longitudinal section of a male strobilus showing male flowers in the axils of bracts.

The stalks of the stamens arise from the edge of a cup-like structure which surrounds the ovule. This may represent a concrescence of their stalks, and it recalls the basal disc of the male sporophylls in *Cycadeoidea* (see Volume III), and may indeed be a link with that extinct genus. The ring contains six vascular bundles, one going to each stamen.

The stamens and the " stigma " grow out from between the bracts and protrude from all the ripe flowers of the strobilus simultaneously.

The Female Strobilus.

The female strobilus is similar to but is larger and blunter than the male, reaching 5 to 7 cm. in length (Fig. 776). The female strobili are not produced in such large numbers as the males. They are borne on very similar inflorescence axes, but the cones are not always sessile. They are bright red in colour.

In the axil of each bract is one female flower, consisting of a single ovule, terminal on a short axis, and enclosed in two coverings (Fig. 777). The inner of these is an integument which is extended, as in the other genera, into a long, narrow tube which protrudes several millimetres from between the bracts. It is only free from the nucellus in the upper part (Fig. 778).

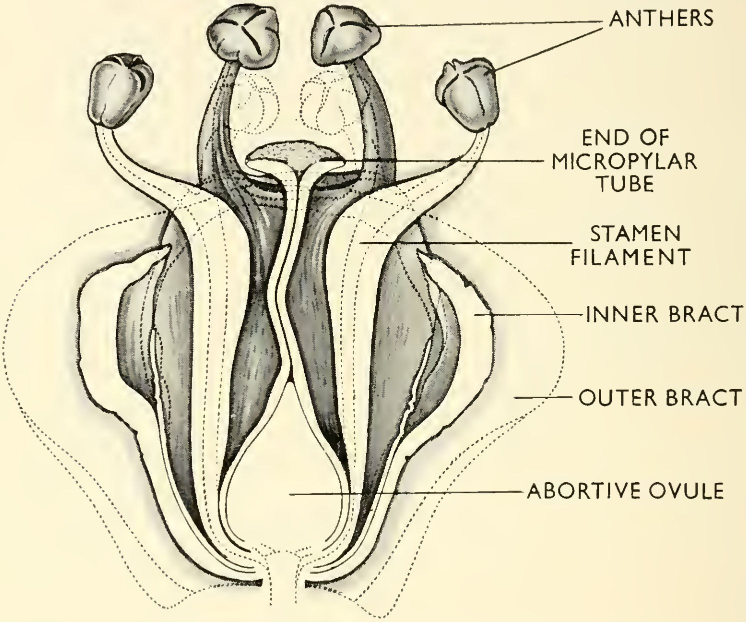


Fig. 775.—*Welwitschia mirabilis.* Longitudinal section of a male flower showing the abortive ovule in the centre.

(*From Church,* " *Phil. Trans. Roy. Soc.,*" *B*, 250, *by permission of the Royal Society.*)

The outer cover, sometimes called the perianth, appears first as a ring at the base of the ovule, but rapidly develops into a two-winged structure which completely covers the inner integument until maturity, when the tube of the inner integument grows rapidly, emerges from a small slot at the top of the outer coat and protrudes beyond the bract of the strobilus (Fig. 779).

It seems not improbable that this two-winged outer coat really represents two fused perianth segments, and this probability is strengthened by the occasional appearance of two small abortive scales, arranged at right angles to the winged structure and external to it, and perhaps making up, with it, the equivalent of the four perianth segments of the male flower.

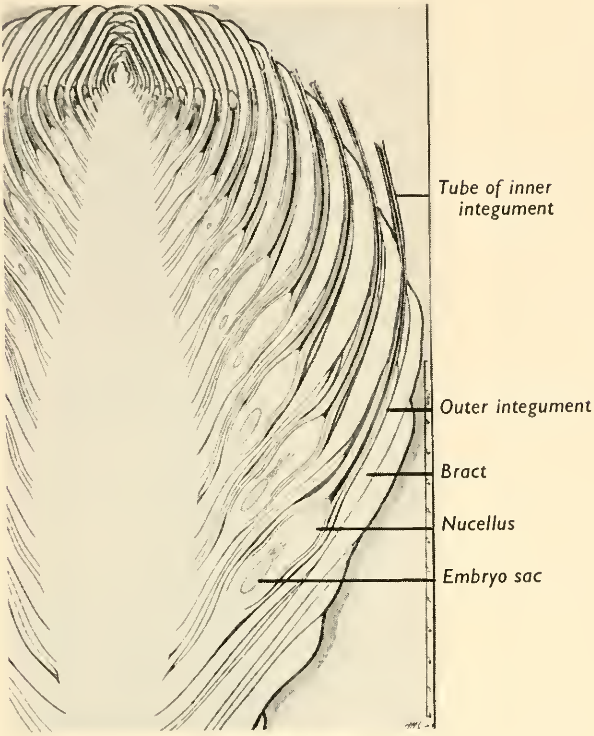


FIG. 776.—*Welwitschia mirabilis.* Longitudinal section of a female strobilus showing ovules in the axils of bracts.

(*From Church, "Phil. Trans. Roy. Soc.," B, 205, by permission of the Royal Society.*)

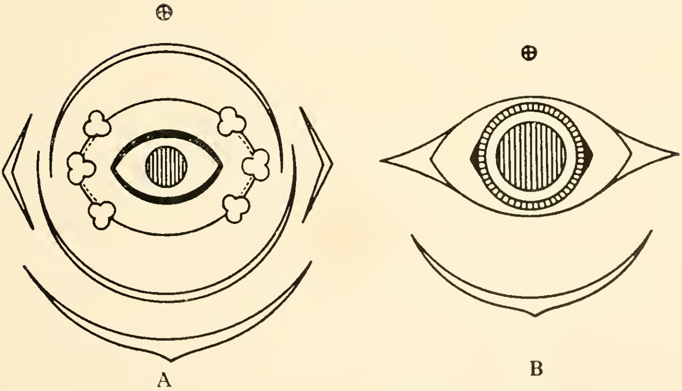


FIG. 777.—*Welwitschia mirabilis.* Floral diagrams of A, Male flower. B, Female flower. (*After Arber.*)

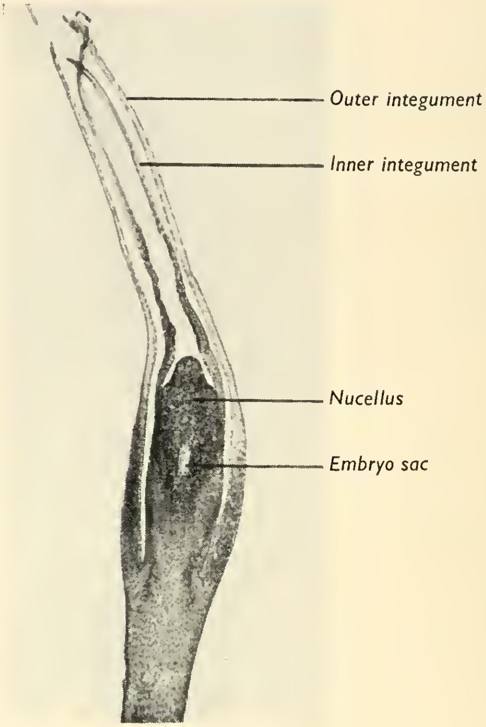


FIG. 778. *Welwitschia mirabilis*. Longitudinal section of an ovule showing the nucellus with embryo sac.

THE MALE GAMETOPHYTE.

The pollen grains of *Welwitschia* are produced in a synangium formed of three fused sporangia at the top of each stamen. The wall of the adult sporangium is single layered, as in many Pteridophyta, and opens by a vertical slit.

The maturing microspore shows three nuclei. One of these is surrounded by dense cytoplasm and is apparently the generative cell, one of the other two aborts, so that the mature grain has two nuclei only, as in the Angiosperm pollen grain before germination. The abortive nucleus may be a remnant of a prothallial cell. The persistent nucleus becomes the tube nucleus at fertilization. Pollination is probably effected by insects.

THE FEMALE GAMETOPHYTE.

The female gametophyte is unique. Only one megaspore mother cell is formed, low down in the nucellus. This seems to form four megaspores, the lowest of which becomes the embryo sac. In it, as it enlarges, nuclear

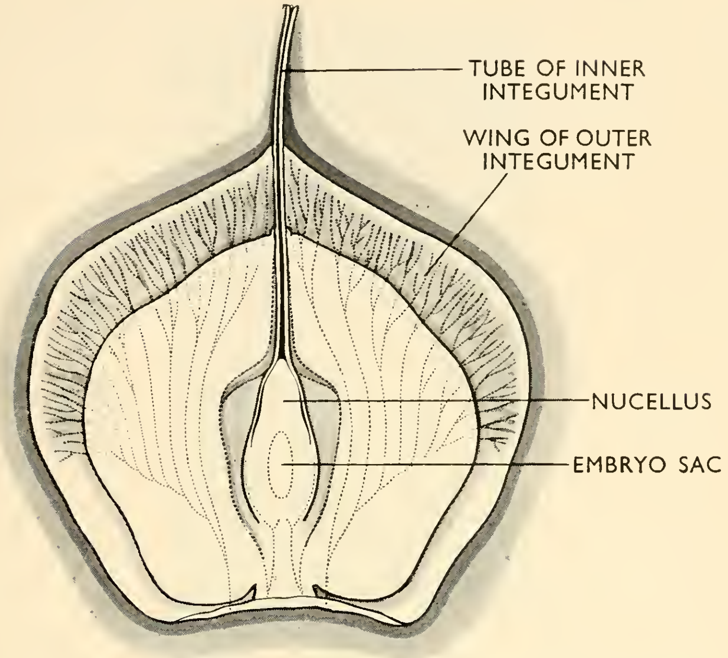


Fig. 779.—*Welwitschia mirabilis.* Longitudinal section of the ovule in the plane of the integumental wings, at right angles to Fig. 778.
(*From Church,* " *Phil. Trans. Roy. Soc.,*" *B*, 205, *by permission of the Royal Society.*)

divisions are simultaneous and are repeated until approximately 1,024 nuclei are formed (*i.e.*, ten divisions). There is no central vacuole, and all the nuclei are evenly distributed throughout the sac. Irregular wall formation then begins, enclosing groups of several nuclei in each cell, but by successive nuclear fusions, which occur sooner in the apical portion, these are finally reduced to one in each cell.

There is no trace of archegonia. Instead, certain cells of the apical part of the prothallus break through the megaspore wall and grow up as tubes into the nucellus, towards the pollen chamber formed at its apex, where they meet and fuse with the pollen tubes descending from germinating pollen grains (Fig. 780). A nucleus from a prothallial tube passes into the pollen tube and *there* fuses with the generative nucleus.

The cytology of all this is highly peculiar. If the nucleus in the prothallial tube has been formed by the fusion of several nuclei it must be polyploid and some reduction of chromosomes must follow or accompany fertilization. In the vegetative cells of the lower part of the prothallus, mitoses occur following the nuclear fusions, and they show at first a very large number of chromosomes, which, however, seems to get less after successive divisions. The details are unknown. The question is, can we still apply the term gametophyte to a structure whose cells are no longer monoploid (x) but polyploid (nx) in nature ?

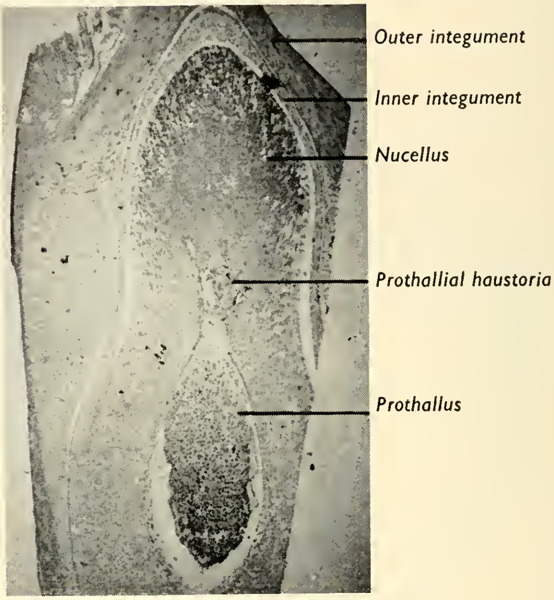


FIG. 780. — *Welwitschia mirabilis.* Longitudinal section of the nucellus and female prothallus at the fertilization stage showing the upward growth of the haustorial tubes into the nucellus.

EMBRYOGENY.

The zygote nucleus divides and the two daughter nuclei become surrounded by walls to form a two-celled pro-embryo. The upper cell is the

FIG. 781.—*Welwitschia mirabilis.* Ripe seeds showing the wings.

suspensor, the lower becomes the embryo. The elongation of the suspensor pushes the embryo downwards, either along the prothallial tube or by direct penetration into the tissues of the prothallus, where it matures. Several separate acts of fertilization may occur, and hence numerous embryos are formed, but normally only one survives to maturity.

The embryonal cell divides into four, and from these the following cells are produced in downward succession :—

1. Twenty-four basal cells, which surround the lower part of the suspensor as secondary suspensors, or inner cortical cells, to which are sometimes added a second or even a third set of outer cortical cells.
2. An embryonal plate of eight cells, from which the mature embryo is formed.
3. A " ring " of sixteen cells of uncertain function.
4. An apical " cap " of eight cells, which is finally discarded.

It is probable that 3 and 4 are only protections for the young embryo as it bores its way down into the prothallus, the physiological analogues of a root cap.

The later stages of embryo development have not been seen, but the mature embryo is straight, has two cotyledons, as we have seen above, and is surrounded by endosperm. The winged outer coat of the ovule develops into a papery structure nearly an inch across and seems to be a means of wind dispersal for the seeds (Fig. 781).

CHAPTER XIX

THE ANGIOSPERMAE: INTRODUCTION TO THE HIGHER FLOWERING PLANTS

The Angiospermae form the highest class of the Spermatophyta or Seed Plants; the Pteridospermae and Gymnospermae being the lower classes. The name is derived from the two Greek words *aggeion*, a vessel, and *sperma*, a seed, and it indicates the character which, above all else, separates them from other Seed Plants; namely, that the seeds are enclosed in an **ovary,** which at maturity becomes a **fruit.** This is a morphological distinction, but biologically they are further distinguished by the fact that the function of pollination is taken away from the ovules and transferred to a special receptive organ, developed by a portion of the ovary and known as the **stigma.**

The ovary is both morphologically and biologically a new organ. How far it and other organs of the angiospermic flower can be compared with the organs of lower plants we shall discuss when we deal with the Flower as a structure. For the present we shall simply recognize that these floral organs, whatever their origin, have become so developed and specialized in the Angiosperms that new names must be used for them.

An angiospermic flower may produce spores of only one kind or of both, but the latter condition (**hermaphrodite** or **amphisporangiate**) occurs so widely and so constantly in the majority of the families that it may be regarded as characteristic, whereas in the Gymnosperms it is only an occasional anomaly. Similarly, the transfer of pollen in Gymnosperms is normally by the wind and only exceptionally by insects or other carriers. In Angiosperms insect pollination is the rule, and indeed the adoption of this method has had so profound an effect on the structure of the flower that it may be regarded as a fundamental factor in the evolution of the class.

Compared with the woody and long-lived strobili of Gymnosperms, the angiospermic flowers are as a rule delicate and short-lived, and are correspondingly more freely produced. The reproductive parts are usually surrounded by an envelope of leafy structures, the **perianth,** which is often highly coloured.

The microsporangia or **pollen sacs** are united into **anthers** which are borne on short stalks or **filaments**; the two structures together form the **stamens.** In the microspore there are no vestiges of a prothallus, only a **tube nucleus** and a **generative nucleus** are present.

The megasporangia are, as in Gymnosperms, enclosed by **integuments,** usually two in number, to form **ovules,** which are enclosed within the **ovary**

wall. A single ovary with its enclosed ovules, together with a short column of ovary tissue, called the **style,** which often supports the **stigma,** form a morphological unit named the **carpel.**

In the embryo-sac there are no archegonia, and no prothallus is formed before fertilization. Only one oosphere nucleus is present, and normally only one embryo is formed. A nutritive tissue develops in the embryo-sac during the growth of the embryo and is called **endosperm.**

Structures of the most varied kinds, which facilitate the dispersal of seeds and fruits, are produced by post-fertilization developments from the ovules and carpels.

The vegetative forms displayed by Angiosperms are most extraordinarily varied and show a very striking contrast to the rather limited and monotonous aspect of the Gymnosperms. They assume every facies known in other groups, from the thalloid type upwards, as well as many peculiar to themselves. Along with this morphological diversity goes the greatest adaptability to habitats, which range through every climate and every sort of situation. During the comparatively short period of geological time which has elapsed since the Angiosperms first appeared in the Cretaceous period, they have spread and multiplied until they have eclipsed all other groups in their importance and have become the dominant race. Yet it seems that all the peculiarities of form, appearance and function which have made possible their conquest of such manifold difficulties can be traced to the three categories of organs, stem, root and leaf, which have shown in this group an unequalled degree of plasticity.

Anatomically the Angiosperms are notable for the presence, except in a very few cases, of xylem vessels, often of large size. Centripetal xylem has disappeared, and with it has gone the truly cauline vascular system which characterizes the Pteridophyta and of which traces survive in the lower Gymnosperms. All the stem bundles are common to stem and leaf. They may pass through more than one internode of the stem, but sooner or later each bundle passes into a leaf. We have argued in a previous chapter that this implies a radical difference of organization between the Seed Plants and the Pteridophyta and that no direct comparisons of their stelar structures are valid (see p. 646).

Many Angiosperms are **annuals,** living for only a single season. They are of rapid growth and have little or no secondary thickening. This new departure in plant habit aids rapid multiplication and dispersal and is, above all, useful to plants which are pioneers in open ground, but it does not usually enable them to hold for long the ground colonized. Like an army of nomads, they are ever on the move.

Another type of habit not found in Gymnosperms is that of the **geophyte,** the plant which perennates by means of underground stems and only sends up a temporary flowering shoot.

The Angiospermae are divided into two series: **Dicotyledons** and **Monocotyledons.** The names are founded on a difference in the number of embryonic leaves or **cotyledons** in the seedling, but this apparently minor distinction is associated with a number of others and undoubtedly marks two types of organization so distinct that some have doubted if they are really of common descent.

The chief distinctions may be summarized thus :—

	Dicotyledons.	Monocotyledons.
Cotyledons	Two.	One.
Stems	Vascular bundles in a ring. Secondary thickening common.	Vascular bundles scattered. Secondary thickening very rare.
Leaves	Venation net-formed, with branches ending freely.	Venation usually parallel. No free ends to veins.
Flowers	Flower parts in fours or fives.	Flower parts in threes.

The Dicotyledons are divided into the **Archichlamydeae,** in which the perianth segments are free from each other and the **Metachlamydeae** (Sympetalae), in which the perianth segments are united into a tube, which is regarded as the higher type. It is associated with more advanced pollination mechanisms and with restricted numbers of floral parts, implying a higher reproductive efficiency. For further details of the classification of the Angiosperms see Volume II.

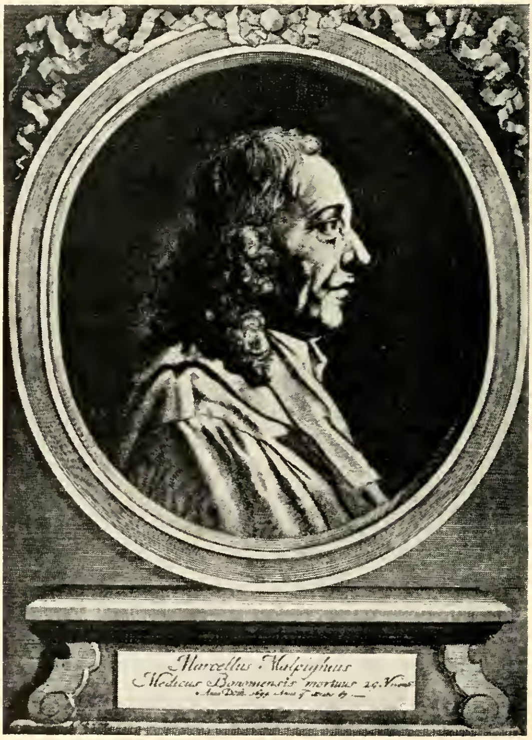


Fig. 782.—Portrait of Marcello Malpighi.

Historical Sketch of Angiosperm Anatomy.

The study of the anatomy of Angiosperms began in the seventeenth century in the hands of two men who worked quite independently of each other; Marcello Malpighi (1628-94) (Fig. 782) and Nehemiah Grew (1641-1712) (Fig. 783). It is a remarkable fact that preliminary treatises by the two men were presented to the Royal Society of London, of which Grew was Secretary, on the same day, 7th December 1671. These were followed by two substantial works: Malpighi's "Anatomes Plantarum Idea" in 1674 and Grew's "Anatomie of Plants" in 1682.

Malpighi was already famous as a human anatomist before he turned his attention to plants, but Grew started out with an economic idea, to find out how timber grew, that commodity being greatly in demand for shipbuilding and threatening, in his day, to become scarce. Grew never reached a correct idea of cell structure and believed that the plant was composed of a lace-work of interwoven threads (hence the term "tissue"), which were no doubt the profiles of the cell walls as seen in sections. He was nevertheless superior to Malpighi in the extent and carefulness of his observations.

Fig. 783.—Portrait of Nehemiah Grew.

The eighteenth century was almost barren in studies of plant anatomy, except for Kaspar Friedrich Wolff (1733-94), who studied meristems and tried to formulate a theory of apical development, and Sir John Hill (1716-75), who published in 1770 a book on the structure of timber, following in Grew's footsteps.

The nineteenth century saw a revival of interest, with the publication in 1802 of a theory of plant organization by C. F. Brisseau-Mirbel (1776-1854), and a work on vessels by J. J. Bernhardi (1774-1850). Their views were opposed by Kurt Sprengel (1766-1833), and the controversy led to the offer, in 1804, by the Royal Society of Göttingen of a prize for an essay on plant anatomy. Three treatises were submitted by the following: K. A. Rudolphi (1771-1832), H. F. Link (1767-1851) and L. C. Treviranus (1779-1864). The two former divided the prize, though posterity has judged the last to have been the best. All three, however, as well as the work of J. J. P. Moldenhawer (1766-1827), have only an historical interest, and it is not till we come to the work of Hugo von Mohl (1805-72) and Carl von Naegeli (1817-91) that we find a recognizably modern outlook founded on a clear perception of cellular structure, based upon the Cellular Theory of organiztion, as it was elaborated by Schleiden and Schwann.

From this time onwards the study of Angiosperm anatomy became widespread. Some work, notably that of the French school, has been influenced only by a spirit of pure anatomical inquiry, but in the great majority of cases the work done has been inspired by other motives, the two principal aims being either physiological or systematic, that is to say that the plant has been viewed either as a functioning mechanism or else as a member of a group of forms related in the evolutionary sense. Relatively little, until recently, has been inspired by the desire for morphological interpretation, and a truly comprehensive survey of Angiosperm anatomy from this standpoint has not yet been achieved.

CHAPTER XX

THE ANGIOSPERMAE: ROOTS

There are several reasons for beginning the study of Angiosperm structure with the root rather than with the stem.

The anatomy of roots is in many respects simpler than that of stems and it is considerably more uniform, perhaps as the result of a rather uniform environment underground, which is in marked contrast with the extreme variability of the conditions affecting aerial shoots. Root anatomy is also more ancient in type than that of stems. Roots preserve, in their primary condition, the actinostelic arrangement of the vascular tissues, which in the lower Pteridophyta is characteristic of both stems and roots. Thus, while the structure of the stem has undergone profound changes in the course of evolution from the level of the Lycopods upwards, the root has altered relatively little and consequently in the Angiosperms its structure contrasts strikingly with that of the stem, which is not the case in the Lycopods.

Furthermore, the relationship of structure to function, the division of functions between tissues and the development of anatomical organization are all matters which are very clearly illustrated in roots.

We may here suggest as a guiding principle in all such considerations as these, that we should look upon structure as arising out of function, not the reverse. A function may exist before there is any anatomical structure particularly associated with it, and it may, in fact, exist along with many other functions in a unicellular organism. The history of structural evolution has been, to a great degree, the history of the way in which conditions of life have induced the localization of functions in the body, with consequent effects on each particular tissue concerned, which we can trace in the observed differentiations of structure.

General Characteristics.

Roots are distinguishable by a complex of characters, and while we should avoid any such idealistic concept as that of a " typical " root, we may say that the organs classed as roots are those which show all, or at least a majority, of the following characters :—

1. Absence of leaves and hence, of course, absence of buds.
2. Possession of a root cap over the apex.
3. Endogenous origin and branching.
4. Phloem and xylem on different radii in the primary structure.
5. A relatively short zone of growth at the apex.
6. Possession of root hairs near the apex.

Additional characteristics, usually found but not essential, are : A positive or neutral reaction to gravity, *i.e.*, a tendency to grow downwards or sideways rather than upwards ; the absence of chlorophyll ; and unsusceptibility to the influence of light.

Of all the above characters the only one which appears to be fundamental and invariable is leaflessness. No true root produces leaves, but some may occasionally produce buds, which grow into leafy stems. On the other hand there are also some true stems which are leafless.

These facts show that even so fundamental a morphological category as that of the root has no absolute value, since it cannot be rigidly defined. An organ can only be judged as to whether it be a root or not on the balance of its characters, and while normal cases present no difficulty there are some organs, like the rhizophores of *Selaginella* and the attachment organs of some parasites, which are very difficult to classify.

FIG. 784.—*Moneses grandiflora.* Root system with temporary leafy shoots. (*After Velanovsky.*)

Roots and stems are by no means indispensable to each other. Roots, for example, can be grown artificially as root cultures. A root apex placed in a sterile culture solution will grow and branch, forming a system that fills the culture vessel, without producing any stems. These root cultures can be propagated vegetatively, through successive culture vessels, for long periods, and form nothing but roots. Practically independent root systems exist also in nature. In the saprophytic family of the Pyrolaceae certain species, *e.g.*, *Moneses grandiflora* (Fig. 784) and *Monotropa hypopitys*, produce at germination nothing but a root, which grows and branches abundantly in the woodland humus and can apparently live perennially in this fashion. It only occasionally produces, endogenously, short, temporary flowering stems, which serve for reproduction.

Contrasted with these " plantless roots " are cases of " rootless plants," especially among floating aquatics. Some of these which have dispensed with roots are otherwise well developed, *e.g.*, *Utricularia* and *Ceratophyllum*, but they also include *Wolffia arrhiza*, the most reduced of all the Angiosperms, which consists of no more than a minute nodule of green cells.

Roots are generally divided into two categories: (1) **primary,** normal or soil roots, which originate from the embryo and usually persist throughout life, and (2) **adventitious** roots, which arise secondarily from stem, leaf or other tissues and which may be either permanent or temporary.

The functions of the primary roots are to anchor the plant in the soil, to absorb water and soluble substances and to serve as storehouses of food materials. The functions of adventitious roots are very various. They may sometimes enter the soil and assume the functions of primary roots. They may even, as in the Monocotyledons, replace the primary roots altogether. On the other hand, they may be modified into climbing organs, stilts or props, thorns, boring organs in parasites and in other ways, which we shall describe later.

Root Systems.

The whole extent of the roots of a plant is called the **root system.** The development of this system differs fundamentally in Dicotyledons and in Monocotyledons.

Among Dicotyledons we find that the primary root of the seedling plant develops directly into the main root, which is positively geotropic, *i.e.*, responsive to the influence of gravity by growing directly downwards. The length and strength of its development depend on the life conditions of the species of plant, and are very varied. In some cases its growth persists throughout life and a large **tap root** is formed, equalling or exceeding the main stem in size, and sometimes swollen into a storehouse of reserve materials. In other cases its growth is slight and its duration is short, so that it is soon lost sight of among the branch roots. The latter type is called the **fibrous root system.** There is roughly an inverse ratio between the extent to which the tap root develops and the amount of branching it displays. Normal soil roots are scarcely ever entirely without branches, but in some storage tap roots the branches are few and relatively small.

Root branches are almost always **endogenous,** that is, they originate from inner tissues (see p. 805) and bore their way through the outer tissues to the surface. This imposes a delay on their appearance externally, so that a distance of several centimetres may intervene between the apex of the main root and the point of appearance of the first branch. This late appearance of branches must have a considerable physiological advantage in the case of a boring organ like a root and should probably be interpreted from this point of view, for although endogenous branching is usually reckoned to be one of the fundamental characters of roots it is, in fact, by no means without exceptions. Adventitious roots in particular often originate exogenously, though their subsequent branching is endogenous.

Attempts have been made to distinguish between different parts of the root system as functionally either anchoring or absorbing systems respectively. Research into the root systems of fruit trees has shown that, at least in young trees, it is possible to distinguish two separate systems. Firstly, an absorptive system of fibrous roots which remain relatively near the surface of the ground and do not grow out beyond the spread of the aerial branches, and, secondly, stout anchorage roots which are few in number and are comparatively little branched. These latter, after running more or less horizontally just below the soil for a distance of several feet around the tree, turn and dive vertically downwards to a considerable depth. These anchorage roots apparently arise only during the early growth of the tree and cannot usually be replaced if they are once damaged. It is a familiar sight to see fruit trees in commercial orchards leaning at various angles and only a few standing vertically. This is probably due to the ploughing of the ground among the young trees to keep down weeds. In so doing some of the anchorage roots may be cut and, since they cannot be replaced by the tree, it loses support and can be readily blown sideways by the prevailing winds.

In general, however, the functional distinction between different parts of the root system is seldom complete. The principal distinction which actually exists is in respect to the reaction to gravity. The main root is the only one which is positively geotropic. Each branch of the main root, *i.e.*, branches of the second order, sets itself at a characteristic angle to the vertical, which is smallest in those nearest to the apex and gradually increases up to a right angle in the branches nearest the surface of the soil, which therefore grow horizontally.

Branches of the third order have no geotropic reaction and simply grow at right angles to their parent roots. These variations in the direction of growth naturally lead to the spreading of the branches away from each other, so that they are well spaced out and permeate the soil most effectively.

Variations of angle and of the rate of growth in different parts of the system naturally cause a good deal of variation in the form of the system and perennial plants can be roughly classified, for instance, into surface-rooters and deep-rooters. Xerophytes, like the Cacti, often show both tendencies in an extreme state, their deep roots penetrating downwards to the permanent water table, which may be 30 ft. down, while their surface roots grow horizontally for many yards, just below the surface, where they may pick up the moisture from every light shower.

Root branches do not appear on the parent root with any regularity, and there is no transverse division of a root into joints as there is in a stem. The branches do, however, form a definite number of longitudinal rows, corresponding to the number of xylem strands in the parent root, except in diarch roots, which normally have four rows. These rows can be seen if a well-branched root is examined endways. The arrangement is due to the place of origin of the branches, as we shall see later.

Root production is not equally vigorous all the year round. In bulbous and other plants with pronounced seasonal activity, root production usually marks the beginning of the active period. Among trees there are generally two maxima, one in spring before the opening of the leaves and one in autumn, from September till the first frosts. Midsummer and midwinter are resting periods.

The amount of branching is greatly influenced by the aeration of the rooting medium. Roots in water or in mud are usually sparingly branched and sometimes not at all. Even in ordinary soils a great difference exists between wet and dry layers, and a deeply rooted plant, which may pass through several different soil zones, may have several distinct layers or storeys of maximum root development, corresponding to the drier and better aerated zones in the soil.

Two distinct types of root system have been observed among woody perennials: the extensive and the intensive. In the former the main root branches grow rapidly with little thickening, and the smaller branches are short lived, so that young roots are only to be found at the periphery of the system. In the intensive type branching is freer and the branches themselves are shorter and more persistent, so that the system contains young roots at all parts and not only at the periphery.

There is no fixed proportionality between the extent of root and of shoot development. It is greatly influenced by external conditions. The roots of dicotyledonous trees have a spread which is roughly equal to the spread of their canopy. Most annuals have, on the other hand, a very restricted root development. Xerophytes show an extreme disproportion, their root systems being often thirty to forty times as extensive as their shoot systems.

It is a matter of extreme difficulty to extract a root system from the soil in anything like its entirety, so that our information on the total extent of the system is limited to a few cases. The work of Weaver in America has, however, shown that it is much greater than used to be supposed. By carefully washing away the soil from the sides of deep trenches, he was able to map complete sections through the root systems of a number of species. Examples of these are shown in Fig. 785. Such sections show that penetration to a depth of 6 or 7 ft. is by no means uncommon and that even a small plant may permeate several cubic yards of soil with thousands of fine rootlets. Lateral movement of water in the soil is normally very restricted, and the plant's chances of gaining a sufficiency of water in dry weather and of food at all times depend upon the completeness with which it can occupy every available portion of the soil volume. Dittmer has calculated that a single Rye plant under favourable conditions may develop a root system with a total length of 350 miles and with a total surface, including hairs, of 7,000 sq. ft. Pavlychenko has estimated that the length of the root system produced by an isolated Wheat plant growing without competition is 45 miles. When planted with others in conventional drills the length is reduced to half to one-third of a mile. The growth of weeds, especially Charlock, may reduce the amount to one-fifth or one-tenth of this. Such figures enable us to realize the intensity of the competition which must exist between the roots of plants living in a close community and how valuable to a plant may be any peculiarity of rooting, *e.g.*, exceptional depth, which may enable it to escape some of this competition.

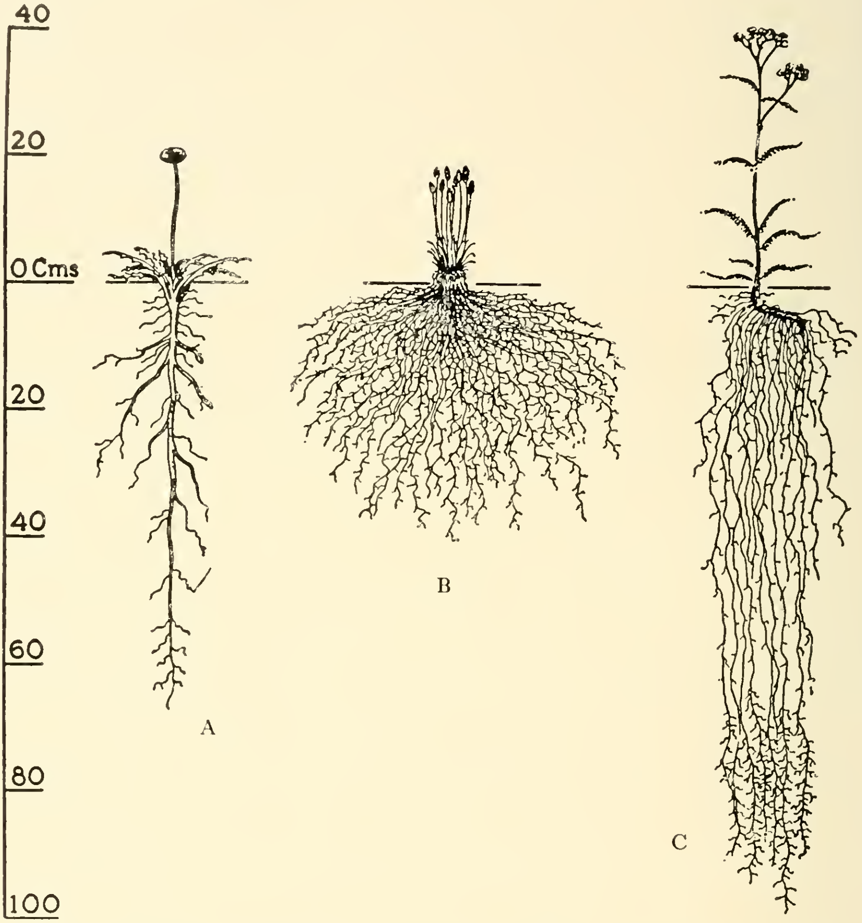


Fig. 785.—Types of root systems. A, *Taraxacum officinale.* Taproot system. B, *Poa secunda.* Fibrous root system. Monocotyledon. C, *Achillea lanulosa.* Fibrous root system. Dicotyledon. (*After Spence.*)

It was mentioned above that the root systems of Monocotyledons differ from those of Dicotyledons. This is due to the early abortion of the main root, which disappears soon after germination in the great majority of Monocotyledons.

In some cases, notably among the Grasses, it may never be formed at all or may abort before germination. The whole root system of the plant consists of adventitious roots arising from the stem, which entirely replace the main root system of the Dicotyledon type. Monocotyledons are thus on the level of the Ferns rather than of the Gymnosperms in this respect.

The first group of these adventitious roots to appear are all coequal in growth and are all positively geotropic, but their branches follow the same rules of growth as in Dicotyledons, producing a fibrous system. Branching is never on the same prolific scale as in Dicotyledons, and in a few Monocotyledons, for example in *Arum maculatum* and in many Orchids, it is entirely absent. The root systems in Monocotyledons are therefore on a relatively small scale, even when the plant, as in the Palms, is tree-like.

Many Monocotyledons have underground stems. Where these grow horizontally they produce adventitious roots throughout their length, but contracted stems, such as bulbs, produce successive crops of roots from the base, each crop lasting only a single season.

SUMMARY OF ELEMENTARY STRUCTURE.*

If one examines the transverse section of a young root (Figs. 786 and 788) an inch or so from the apex, one may note the following typical arrangement of the tissues :—

1. A surface layer of cells, the **piliferous layer,** most of whose cells bear on the outer side tubular prolongations, the short-lived **root hairs,** which may be several millimetres long and have very thin walls.
2. A layer of cells next to the piliferous layer, which becomes the surface layer when the former has been shed. This is called the **exodermis.**
3. A broad **cortex** of parenchyma cells, usually filled with starch grains.
4. A well-marked **endodermis.**
5. A rather small **stele,** enclosed by the endodermis.
6. The stele is surrounded by a layer of thin-walled cells, the **pericycle,** which lies next to the endodermis.
7. A number of groups of **xylem** cells, with the **protoxylem** outwards, *i.e.*, **exarch.**
8. An equal number of groups of **phloem** cells, *alternating* with the xylems and having their **protophloems** outwards.
9. A small central area of parenchyma, the **conjunctive tissue,** which is sometimes replaced by metaxylem.

Dicotyledons usually have two (diarch), four (tetrarch), or five (pentarch) xylem groups, less frequently three (triarch) or seven (heptarch), and rarely more. Monocotyledons have greater numbers (polyarch), sometimes as many as thirty, surrounding a relatively large conjunctive tissue (Figs. 787 and 789).

This statement of elementary structure will serve as a basis for the following more detailed consideration of anatomy.

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* This section and the corresponding sections on the stem, the leaf and the flower are intended as outlines for the benefit of the elementary student.

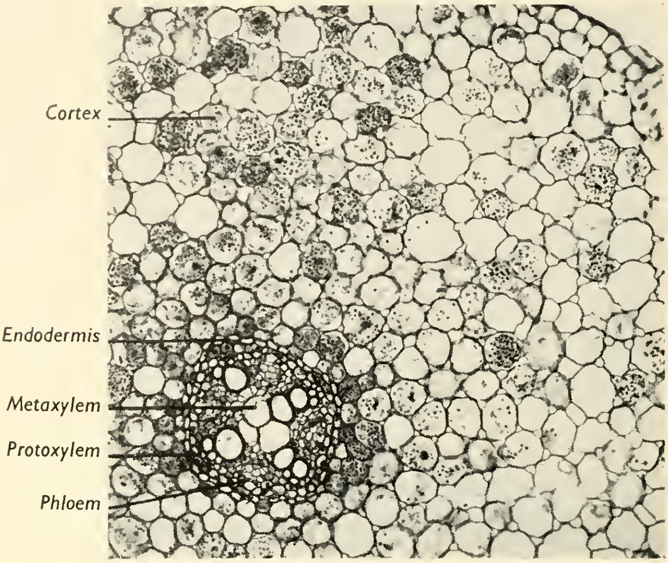

FIG. 786.—*Ranunculus repens.* Transverse section of root showing wide cortex containing starch grains, and small tetrarch stele.

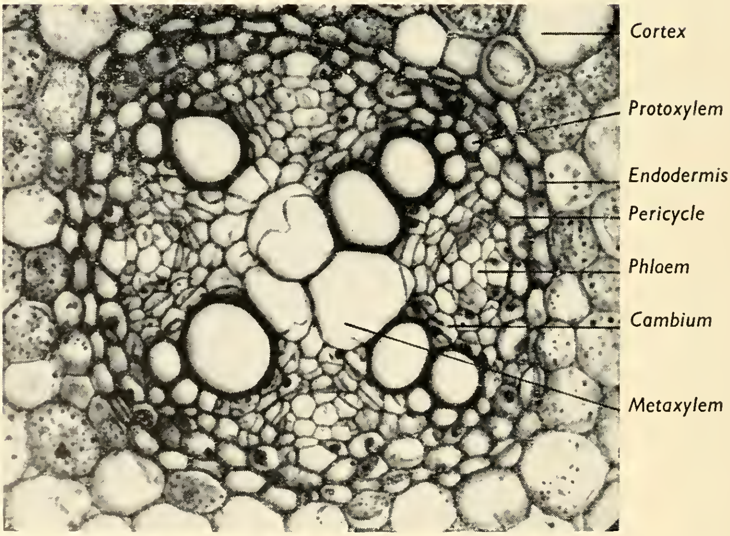

FIG. 787.—*Ranunculus repens.* Enlarged view of root stele showing metaxylem in course of centripetal differentiation.

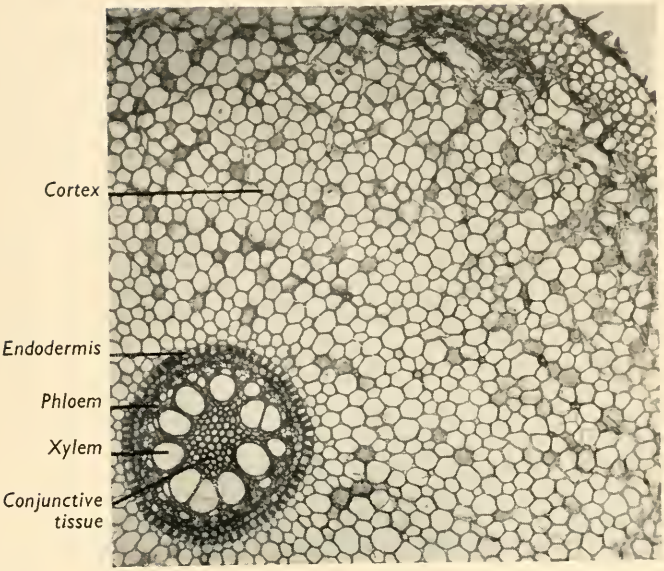

FIG. 788.—*Iris germanica.* Transverse section of root showing wide cortex with suberized outer zone and small polyarch stele.

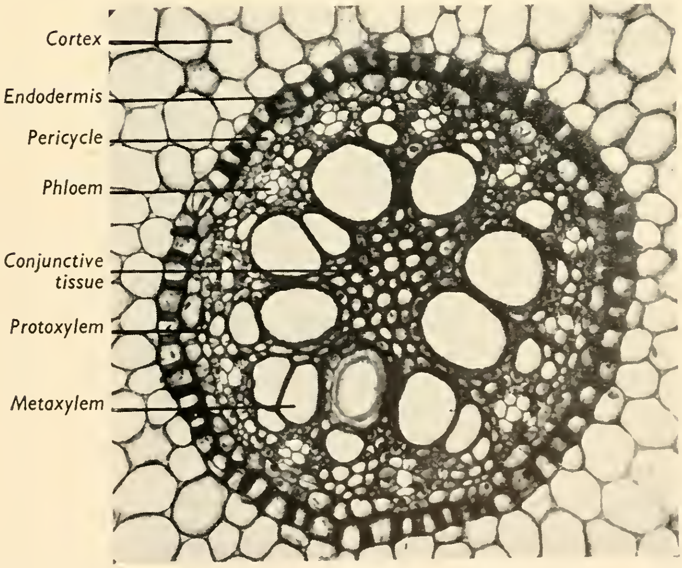

FIG. 789.—*Iris germanica.* Enlarged view of root stele.

MERISTEMS.

The meristem of the root is very different from that of the stem. The outgrowth of leaves from the latter produces more complex conditions, which we shall have to consider later, and the morphology of the meristem is much more varied. The root apex forms a rounded cone, the tip of which consists of the **root cap** or **calyptra.** The actual meristem lies beneath this covering and so at some little distance from the surface.

No single apical cell can be found ; instead there is a cluster of **initial cells,** the fundamental meristem, from which radiate the concentric zones of cells, which form the permanent tissues and are easily recognized in longitudinal sections. The group of initials usually consists of several superimposed layers of cells, but this is very variable. It constitutes the true meristem and its cells are closely coherent, with no air spaces between them and they contain no vacuoles. They have a twelve-sided or fourteen-sided shape, which is that formed when plastic spheres are pressed together in a closed space. This differentiates them clearly from the developing, but still meristematic young tissues, whose cells are regularly rectangular.

In 1868 Hanstein put forward a theory of germinal layers, or **histogens,** at the apex of the stem and root. He distinguished a central core or **plerome,** consisting of more or less elongate cells, around which lies a shell of **periblem** consisting of several concentric layers of rectangular cells. The outer layer or **dermatogen** is normally only one cell thick and is distinguished by the uniformly anticlinal division of its cells (*i.e.*, the division planes are perpendicular to the outer surface).

This is in fact no more than a statement of what observation shows us, and such layering necessarily arises when the initial group has at least three layers, superimposed vertically. Hanstein's theoretical limitation of these layers as " germinal," was influenced by the prevailing studies on animal embryos. He considered that the plerome produced the stele, the periblem gave rise to the cortex and the dermatogen produced the epidermis. Careful study has shown that these limitations are not generally fulfilled. As we shall see, the histogen theory has been dropped in the interpretation of the stem apex. It has still, however, a descriptive value in the root apex (see Fig. 790), especially in connection with the origin of the root cap. The surface layer of the root is not, however, an epidermis and the outer germinal layer is not continuous over the apex as the dermatogen is in the stem, so that it is better to adopt for it the term **protoderm.** The plerome cells cease dividing and begin elongating earlier than those of the periblem, and the differentiating zones of the periblem and plerome are fairly easily distinguishable (Fig. 791).

THE ROOT CAP.

The root cap is usually described as arising from a special histogen layer, the **calyptrogen.** This is true in many cases, but not in all. The most

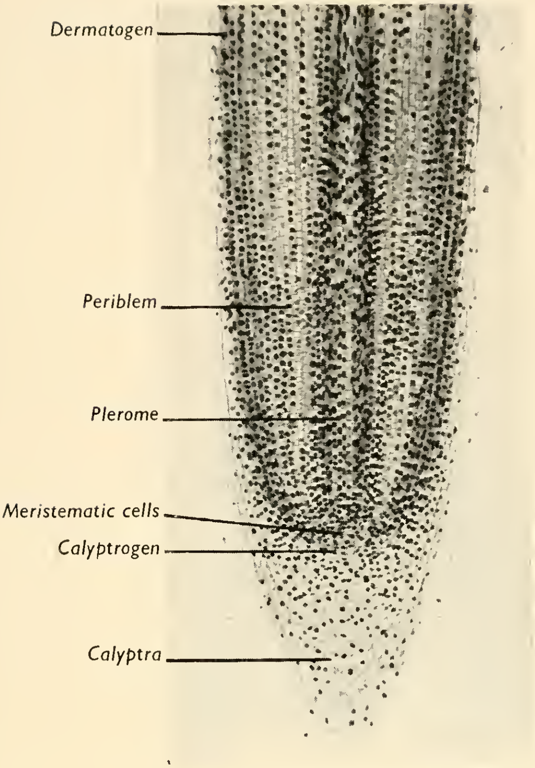

FIG. 790.—*Vicia faba.* Longitudinal section through the root apex showing apical meristem, germinal layers and root cap.

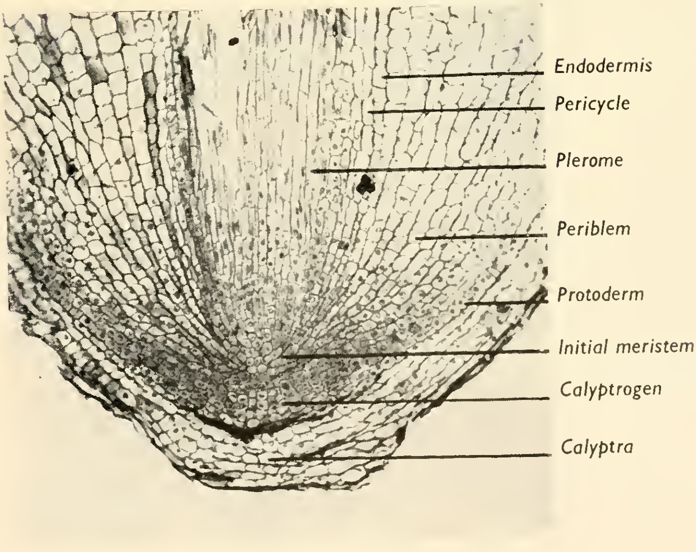

FIG. 791.—*Aucuba japonica.* Longitudinal section through the root apex.

definite calyptrogen is formed in a few Monocotyledon families, such as the Gramineae, in which it is completely distinct from the other meristematic zones, so that the root cap is really an independent structure (see below). In the majority of Dicotyledons the calyptrogen is formed by the division of the protoderm cells or from the protoderm and periblem together, so that the root cap must be regarded as an outgrowth of these tissues. Among the Leguminosae and the Liliaceae, however, there are a number of genera in which no distinct calyptrogen exists, and the root cap arises from the same initial group as the other root tissues, with which, consequently, it is more or less directly continuous. Even in these cases the protoderm often contributes to build up the root cap tissues. From the point of view of evolution it seems probable that the root cap is a development from the protoderm and that the normal dicotyledonous condition, described above, is the most primitive.

Before leaving the origin of the root cap, mention should be made of the condition in lateral roots and in adventitious roots which develop endogenously. Here a protective pouch is formed over the apex of the young root by the endodermis of the parent axis, which becomes meristematic at this point. Normally this pouch is later sloughed off, but in many Monocotyledons, *e.g.*, the Gramineae, no true calyptra is formed by the root itself and the pouch remains as a permanent structure, growing from its own inner layer, which constitutes the calyptrogen. The remarkable large root " cap " in *Lemna* is of this type (Fig. 792).

Fig. 792. — *Lemna minor*. Apex of root showing abnormally large root cap.

The cells of the root cap are cut off from the meristem in radial rows, but they very quickly become vacuolated and rounded off, the walls at the same time becoming mucilaginous. They are so loosely attached to each other that they are easily rubbed off by contact with the soil. Thus the life of each cell is short and the tissue is continuously renewed.

A small central core or **columella** of cells in the root cap contains starch grains, to which the special name of **statoliths** has been given, as they have been regarded as the means by which the root orientates itself to gravity.

The cells of the root apex are much less permeable to water than those of the stem apex, and it may be due to this that the initial group is internal and nearer to the apex of the vascular system than in the stem. The same fact may also explain the rapid maturity and short life of the external tissues of the cap.

The protective function of the root cap is illustrated by the remarkable power of penetration shown by roots, not only in soil and rock crevices, but also in boring through other plant tissues. The adventitious roots of some plants bore their way downwards through the cortex of the stem to the ground level. Tissues of neighbouring plants are also sometimes penetrated, and the authors have observed the root of a Broad Bean seedling which had bored through the main root of another Bean seedling close by.

Immediately behind the initial group there lies a zone in which cells are vacuolating but are still in rapid division. Most of these divisions are anticlinal, the concentric layers maintaining their distinctness and appearing in longitudinal sections as long files of cells leading backwards from the initial group. Spaces containing air soon appear between the cells.

About 3 mm. upwards from the apex the cells enter a phase of elongation, and divisions become rarer. This elongating zone is very short, only 1 to 2 mm. long, but it is here that practically all the growth in length of the root takes place. It is a rapid and rhythmical process, alternating in phase with the cell divisions in the zone below. The maximal periods for cell division are round about midnight and midday, the maxima of elongation lie about halfway between these times.

The whole force of elongation goes into the longitudinal extension of the root, as there is no complication due to leaf formation, and root extension is consequently much more rapid than that of the stem, a fact which we see reflected in the enormous total lengths of root which may be produced. Under natural conditions it takes place in the dark, which favours cell elongation, but it does not seem to be affected by light of moderate intensity, to which roots are usually insensitive. Longitudinal extension may be regarded as the underlying principle of root growth, in contrast to that of the stem, which is superficial extension, involving leaf formation.

Root Hairs.

The surface layer of the young root develops from the protoderm. It has no cuticle and the cells remain in active division farther back from the apex than those of the internal tissues. In the zone of cell elongation they elongate in common with other cells, and immediately above this zone the outgrowth of root hairs begins (Fig. 793) from which this surface takes the name of the **piliferous layer** or **epiblem.** Not every root produces hairs. As has been pointed out above they are less frequent in water plants and sometimes altogether absent, but it has often been observed that the roots of water plants which are normally hairless will produce hairs if they penetrate soil or even pure quartz sand. A contact stimulus seems to be indicated. Exactly the opposite, namely hair production only under well-aerated conditions, is found, however, in *Nasturtium* and some other aquatics, so that the matter is evidently not simple.

Fig. 793.—*Sinapis alba* (White Mustard). Primary root of seedling with root hairs.

Carex shows dimorphism, the thick primary roots being hairless and the finer secondary branches hairy.

A number of Monocotyledons, for example *Elodea*, *Potamogeton* and *Carex*, develop special hair-producing cells or **trichoblasts,** which remain short while the rest elongate, and only from these short cells are hairs formed.

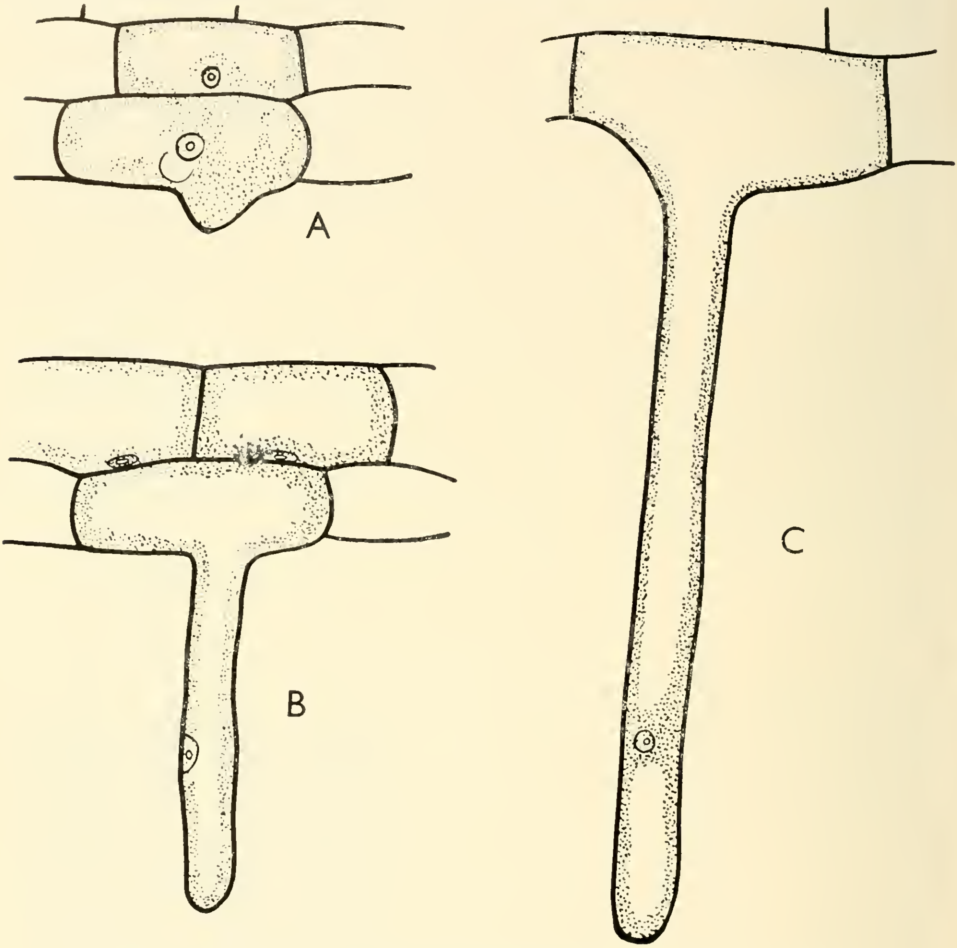

FIG. 794.—Stages in the development of a typical root hair from a cell of the piliferous layer.

The formation of these short trichoblasts is an example of the rare phenomenon of unequal cell division. Most plants, however, develop hairs from the majority of the superficial cells, the proportion varying between 60 and 100 per cent., even in the same species under uniform conditions. A few species have the habit of forming hairy regions in successive zones, but normally hair formation is continuous.

Each hair consists typically of an unbranched cylindrical tube in open connection with its basal cell (Fig. 794). There is a thin lining of cytoplasm with a denser aggregation near the apex, in which the nucleus usually lies. The full development only takes a few hours and the length reached may vary between 0·2 and 5 mm., or in damp air even more. In the soil the primitive form is greatly distorted by contact with soil particles, to which the wall of the hair adheres firmly and the hair may even become branched.

The growth of these hairs seems to be correlated with the stoppage of expansion in the cells which bear them. It is to be observed that they appear just above the principal elongating zone of the root, that is to say, their appearance coincides with the cessation of cell elongation. Furthermore, if roots of the same species growing under different conditions are compared, a greater production of hairs is associated with shorter basal cells, while the trichoblasts, in those species where they are specially formed, are always much shorter than the other surface cells. The appearance of the root hairs behind the zone of cell elongation prevents their being broken off by the forward growth of the root.

The growth of the hair is preceded by a change in the middle lamella and in part of the outer wall of the basal cell, from pectic acid to Calcium pectate. The tip of the young hair is formed from a portion of wall which contains less Calcium than the rest and is in consequence softer and more delicate. The hair grows entirely by the stretching of this soft tip, and the fresh substance added to it from the protoplasm is hardened by addition of more Calcium on the sides of the hair. Oxalic acid, which hinders pectate formation, or an excess of Calcium, which has the opposite effect of causing complete pectate formation all over the wall, both prevent the formation of hairs. Some older hairs, especially in *Gleditschia* and *Eupatorium*, show some lignification and may persist even on the older roots. In the Commelinaceae persistent root hairs develop from the exodermis after the normal root hairs have disappeared.

The life of a root hair normally ends as rapidly as it begins. Shortly after reaching full length the hair dies and drops off, taking with it the surface cell from which it grew. In this way the whole of the piliferous layer disappears, leaving the hypodermal layer, called the **exodermis**, as the new surface of the root. The cell walls of this layer are often impregnated with fatty substances.

The growth of root hairs obviously increases the total surface of the root, which may be important from the point of view of absorption. Actual measurement shows that this increase of surface is exaggerated by the eye. It may be as much as ten times, but it is more often of the order of three to five times. Some of the higher ratios are found among aquatics, and this raises the question why it should be so, as they apparently need the increased absorptive capacity less than do land plants. It may be pointed out that although root hairs increase the absorptive surface in contact with the soil, they do not affect the absorptive capacity of the root to a corresponding extent, since all materials absorbed by them must pass into the root itself through the base of the hair. Thus the effective assimilating surface of the root is unchanged by the development of the hairs. Priestley has suggested that perhaps absorbed water is carried through the cell walls rather than through the cells, and that the endodermis is the real limiting layer in this operation. If that be so, increase of the outer surface is not of great significance in water absorption, but it may nevertheless play an important part in the absorption of dissolved salts, which penetrate by diffusion through the cell surfaces. This would be especially the case in a watery medium, where the concentration of salts is often lower than in the soil.

THE CORTEX.

The cortex in roots is usually wide and the cells are rounded, so that the intercellular air spaces are well developed even in land plants. The cortical cells in many roots, especially in Monocotyledons, are arranged in regular radial rows, and the air spaces when formed are usually also radially arranged (Fig. 795). In water plants the air spaces of the inner portion of the cortex become very extensive and a large aerating system is formed.

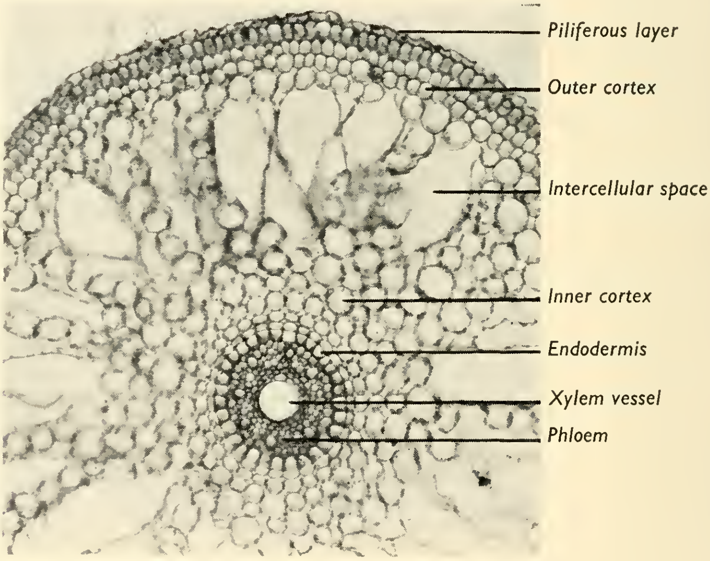

FIG. 795. *Phragmites communis* (Great Reed). Transverse section of the root showing lacunar cortex and reduced vascular system.

The **endodermis** is morphologically the innermost layer of the cortex, not the outermost layer of the stele. The demarcation of the stele at the growing point depends on the formation of the pericycle layer ; the endodermis is differentiated later.

The first and most characteristic stage in the development of endodermal cells is the appearance, at a very early period, of the **Casparian band,** which surrounds each cell like a belt, on the radial and horizontal walls. This belt is usually narrow, but it may sometimes cover the whole radial wall. It is due to an impregnation of the middle lamella with a substance resembling lignin but of uncertain composition. It also contains fatty materials. This band maintains the cohesion of the endodermal cells, so that no intercellular spaces are formed between them and as it is impervious to water it entirely prevents any capillary movement through the endodermal walls, either to or from the stele. Water passage through this layer must therefore be osmotic. The region of the band in the wall normally appears convoluted, but it is not clear whether this is always a natural consequence of a difference in growth rates or whether it is simply an appearance due to the release of strains in sections cut for microscopic observation. The protoplasm adheres closely to the Casparian band and does not leave it even when the cells are plasmolyzed.

Endodermal cells are somewhat elongated, in comparison with cortical parenchyma, and the bands surrounding them form a continuous meshwork, which gives the endodermis considerable mechanical strength. It is in effect a physiological boundary which controls the lateral movement of water, and perhaps more importantly, of solutes. From the point of view of the water supply to the upper parts of the plant it is the functional absorbing surface of the root, as it is here that the water enters the vascular system. Indeed in many grass roots the cortical tissues are only short-lived and the endodermis becomes the actual as well as the functional absorbing surface.

The primary condition of the endodermis is often followed by further changes. Firstly there is the deposition of a suberin layer over the inner surfaces of the cells, and secondly a thick deposit of cellulose mixed with lignin. This thickening is commonest in Monocotyledons and may occur only on the inner and side walls (the C-type) or all round the cell (the O-type). In a few cases this renders the endodermis completely impervious, but in most cases certain unthickened cells remain, directly opposite the protoxylems, which are called **passage cells** (Fig. 796). Through these some interchange of materials is kept up even in the older roots.

The typical endodermis is especially characteristic of roots, but its development seems to be determined to some extent by external factors. It is usually most thickened in plants growing in places where the water supply is scanty or variable, where its mechanical protective strength may be valuable. It is rarely present in stems, except in some aquatic plants, in which absorption may take place through the stems as well as the roots, and it may be that it is only essential in absorbing organs, where its restrictive nature assists the development of the water tension in the stele, by means of which water is raised to the leaves. Little is known, however, about the factors which determine its presence or absence. For example, it is absent from the roots of some, but not all, aquatics and it may, on the other hand, in some grasses, such as *Festuca*, be present in the stem and persist right up into the leaves. There can be little doubt, however, that it is important chiefly as a physiological limiting layer and that it is not simply the morphological boundary of the stele.

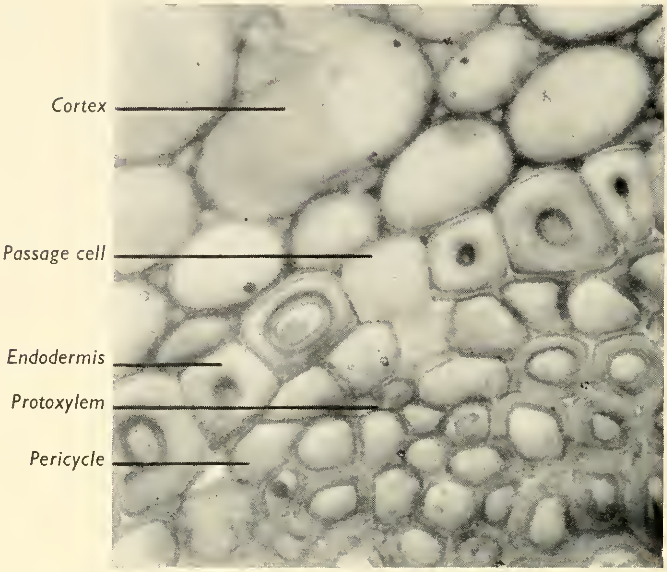

FIG. 796.—*Cypripedium sp.* Transverse section of root showing O-type endodermis with thin-walled passage cell.

THE STELE.

Inside the endodermis there is a **pericycle** consisting usually of a single layer of thin-walled cells which retain their meristematic capacity for division, both radially and longitudinally, even in the older root. It is from this layer that the initials of lateral roots are formed and it contributes to the cambium when secondary growth begins.

The pericycle is differentiated very early at the root apex, and normally from the same initial or initials as the rest of the central cylinder. The whole mass of the central cylinder in its early state is to be regarded as **procambium.** Pith is often absent, the xylem then developing to the centre of the root, but when it is present it develops from the same common mass of tissue as the vascular elements. Xylem and phloem arise in the central cylinder, the first phloem elements preceding the xylem by a considerable distance.

Although procambial elements are usually narrow and long, most Monocotyledons and some Dicotyledons show, among the narrow elements, longitudinal rows of large cells of squarish outline, which are the mother cells of the large vessels. They appear quite close to the apex, but in spite of this early differentiation they do not develop lignified walls, or lose their protoplasm until after the protoxylem, which appears near the periphery of the plerome, has completed its development. In transverse sections of young roots, these large elements may be seen, still unlignified, lying near the centre of the stele, at a stage when the outer xylem cells are completely matured.

The first xylem elements to mature are those lying nearest to the pericycle (Fig. 797) or, in the Grasses, in the pericycle itself. These are called the **protoxylem**, and because they are external and the later-formed elements develop successively in a **centripetal** direction, the root stele is said to be **exarch.**

The difference between the protoxylem and the later **metaxylem** is hard

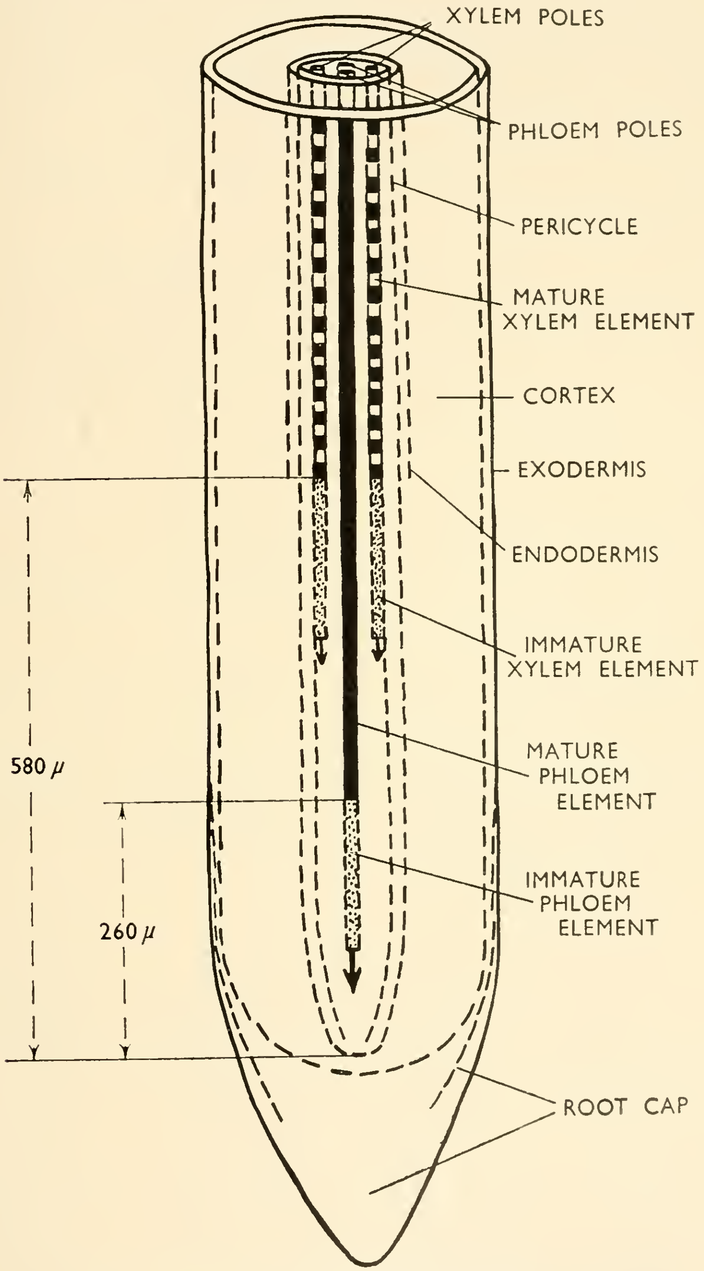

FIG. 797.—Diagram of the course of differentiation in a root apex. (*After Esau.*)

to define exactly. Protoxylem elements are always narrow, and because they are formed in tissue which is actively elongating, they become greatly stretched and are sometimes disrupted more or less completely by the growth forces of the cells around them. Metaxylem matures only after elongation of the tissues is complete and so is not subjected to stretching, though the cells may grow apically and become very long. Protoxylem cells usually have annular or spiral thickening and the later-formed metaxylem cells are usually pitted, but there is no hard and fast boundary line to be drawn on this character. It seems best to use the term protoxylem in a purely topographical sense, for those xylem elements, whatever their character, which appear first and thus fix the pattern for the subsequent differentiation of the rest of the primary xylem.

The phloem also may be differentiated into **protophloem** and **metaphloem,** the former having narrow sieve tubes which are usually soon crushed out of existence. Here there is even less evidence of histological distinction than in the xylem, and the terms are purely topographical. The protophloem develops next to the pericycle, at the same time as the protoxylem, while the metaphloem is contemporaneous with the metaxylem.

BRANCHING OF ROOTS.

The normal mode of branching is monopodial, the main root persisting and giving off laterals. Very few exceptions are known among Angiosperms. The tuberous roots of Orchids are often dichotomous or polytomous, and mycorrhizal roots are almost always dichotomous, but these are the only known cases.

Among the Lycopodiales dichotomy of roots is the rule, and it was probably also the case in the primitive axis from which both roots and shoots have been evolved. There are grounds for holding that it is the most primitive form of branching. It is interesting therefore to note the suggestion of von Goebel that endogenous branching may have arisen by the modification of a primitive dichotomy. The four sketches given in Fig. 798 are sufficient explanation of the hypothesis.

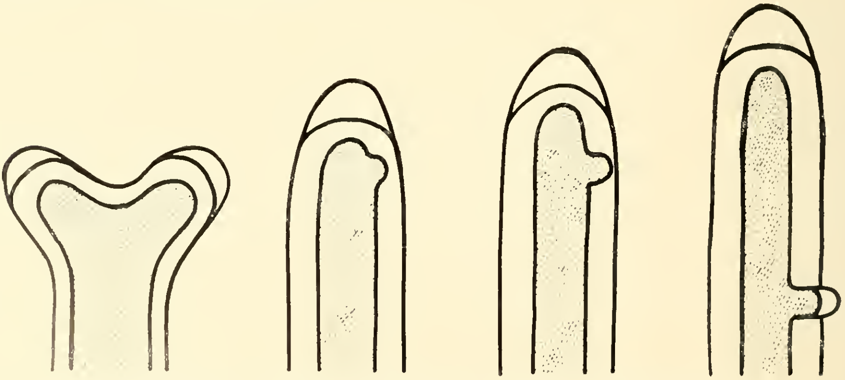

FIG. 798.—Diagram to illustrate the theory of the origin of endogenous branching from a primitive dichotomy. (*After Goebel.*)

The lateral branches of the root originate **endogenously** from the margin of the stele, and this again is a rule with very few exceptions, though it is well to realize that exceptions exist even to this most characteristic feature of roots.

Biologically the endogeny of root branches may be interpreted as protective. There being no leaves to form a protective bud, the main root has to rely upon the covering afforded by the root cap, while the external tissues of the parent root serve the branches in the same way until they have formed their own root caps. Moreover this method of origin delays their appearance at the surface, and they may be several centimetres behind the apex of the main root before they break out. Thus the forward growth of the main apex is not hindered by horizontal outgrowths, nor is the physiologically important zone of the root hairs interrupted. Exceptions to this rule may be found among water plants, where the above considerations do not apply. For example, in *Eichornia*, the Water Hyacinth, the branch rudiments are formed in the apical meristem and emerge almost immediately from the parent root.

The outer layers of the root become differentiated and specialized at a very early stage, while the inner layers retain their embryonic character much later, especially the pericycle. No doubt this is associated with the later as well as with the endogenous origin of the branches.

In all types of root having more than two xylem groups the laterals originate opposite the protoxylems. There are thus the same number of longitudinal rows of branches as there are xylem groups in the main root. Diarch roots are a notable exception to this rule. Their branches form four rows opposite each of the spaces between the xylem and phloem groups. A special feature of diarch root branches is that in Vascular Cryptogams the xylem plate is typically horizontal, whereas in Angiosperms it is always vertical. The Grasses and other Monocotyledons having a large number of root xylems do not, however, produce branches opposite all of them.

When a root branch is initiated the pericycle cells divide both radially and tangentially, a disc-shaped body of cells being formed, which increases into a rounded boss and pushes the endodermis outwards in front of it. The endodermal cells also begin to divide and they form a cap over the developing branch apex. This portion of the endodermis breaks away from the rest and is carried outwards through the cortex by the developing branch. The cortical cells disintegrate in front of it, and van Tieghem called the sac thus formed the "digestive pouch," attributing it to enzyme action. This is doubtful, the action being probably due purely to mechanical pressure. Meanwhile the branch apex is differentiated into histogen zones (Fig. 799). It develops its own root cap, and vascular elements differentiate acropetally in its plerome, beginning at a point in contact with the corresponding tissues of the parent root. On finally emerging through the ruptured exodermis, the endodermal cap is sloughed off and the young apex remains covered by its own cap, except, as mentioned above, in some Monocotyledons, where the branch roots form no calyptra of their own.

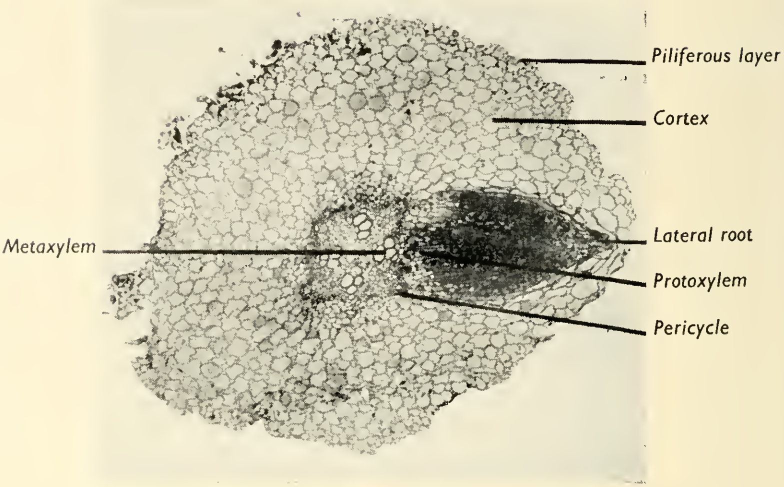

Fig. 799.—*Vicia faba*. Transverse section of a root showing the endogenous origin of a lateral root from the pericycle opposite a protoxylem group.

Secondary Thickening.

When the differentiation of the primary metaxylem is complete, or nearly complete, a **cambium** makes its appearance, in roots which undergo thickening. This includes most roots except those of Monocotyledons and those of short-lived annuals and of most aquatic Dicotyledons.

The cambium in roots is always definitely a secondary structure, that is to say, it is not traceable directly to the apical meristem, but arises by the alteration of mature parenchyma cells. It appears at first in a number of disconnected arcs around the inner margins of the phloem groups (Figs. 800 and 801).

We shall consider the details of cambial growth under the stem (see p. 891), so at present we may simply say that these cambial strips actively produce new, secondary xylem cells on their inner sides and a relatively small number of secondary phloem cells on their outer sides. But whereas these phloem cells are contiguous to the primary phloems, the secondary xylem lies between the primary xylems, and on the same radii as the phloems.

The cambial arcs soon extend laterally until they touch the pericycle at their extremities. At these points the pericycle cells become meristematic and form links round the outside of the protoxylems, thus uniting the separate arcs of the cambium into a continuous band, running inside the primary phloems and outside the primary xylems.

By continued and rapid formation of secondary xylem inwards, the concave arcs of the cambium zone move outwards, carrying the phloems with them until the band ceases to be sinuous and becomes a perfect circle.

Opposite the primary xylems the cambium only forms parenchyma cells,

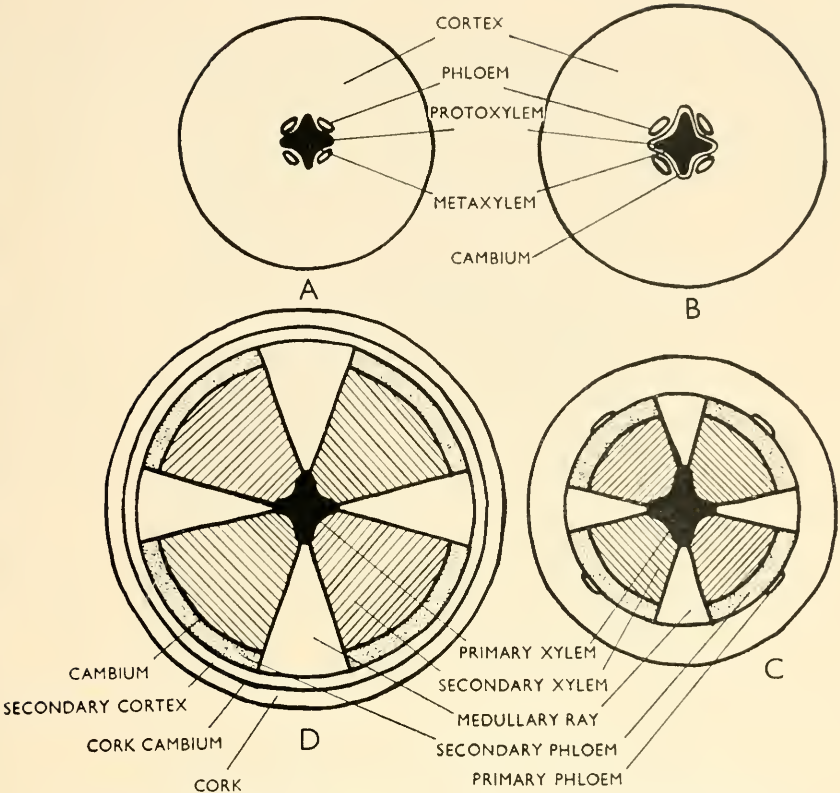

FIG. 800.—Diagram to illustrate the process of secondary thickening in a dicotyledonous root.

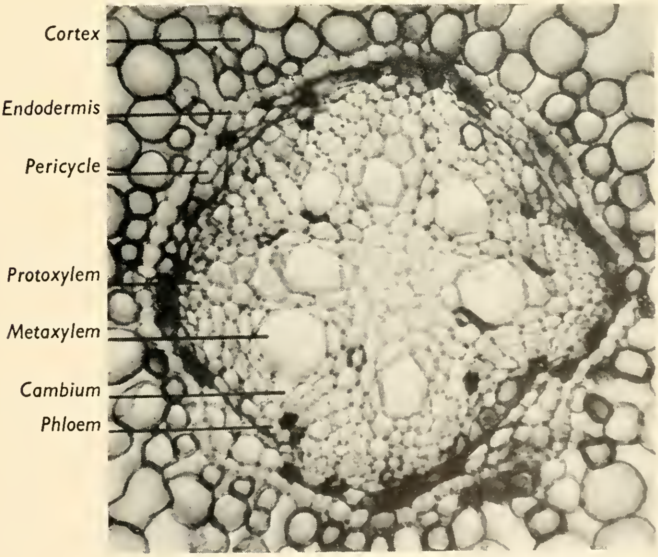

FIG. 801.—*Salix sp.* Transverse section of the root stele showing the beginning of cambium formation.

so that broad **medullary rays** mark the position of the primary xylems in the old root. As growth continues centrifugally these rays may be gradually narrowed, and in the outer zones of old roots they may be reduced to one cell in width. This implies a gradual lateral extension of the broad wedge-shaped masses of secondary tissues so that there is eventually a practically continuous zone of secondary xylem and secondary phloem (Fig. 802).

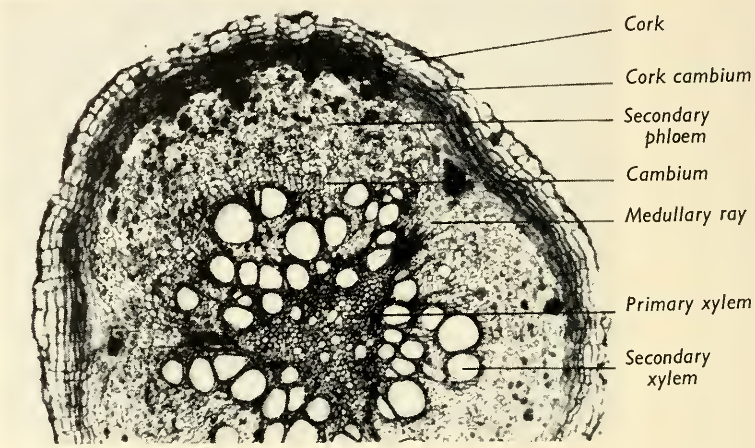

FIG. 802.—*Ulmus procera.* Transverse section of an older triarch root showing secondary thickening.

Exceptions sometimes occur in the roots of herbaceous or of climbing plants, such as *Cucurbita*, in which the cambium arcs never join into a continuous ring, with the result that the wedges of secondary tissue remain distinct and the primary medullary rays are not closed (Fig. 803 and 804).

Cambial growth ceases during the winter, though the cambial cells do not disappear. When growth is resumed in the spring the discontinuity in the growth of the wood is usually evident, so that **annual rings** may be seen in older roots.

The nature of the secondary wood varies greatly. In woody plants it is usually compact and highly lignified, consisting chiefly of tracheids, with small numbers of vessels and parenchyma cells, but in herbaceous plants it may be very loose, groups of vessels and tracheids being mingled with abundant parenchyma sometimes in a wholly irregular fashion.

The elements in secondary wood, especially in the compact type, are usually arranged in radial rows, corresponding to their origin from cells of the cambial ring, an arrangement which distinguishes them from primary xylem. Besides the large primary medullary rays there are many **secondary rays,** one cell broad, which are formed in successive annual rings. New rays are formed intermediate between previous rays, so that the average distance between them remains approximately equal, in spite of the increasing diameter of the root.

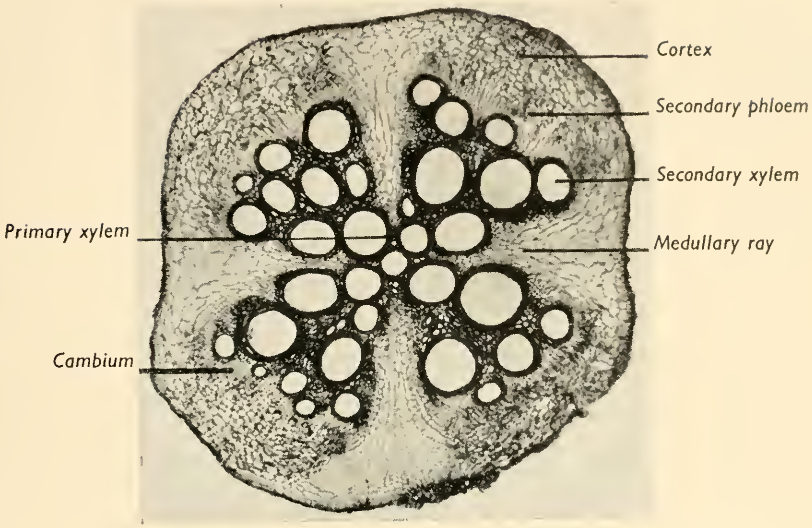

FIG. 803.—*Cucurbita pepo.* Transverse section of a tetrarch root showing secondary thickening. Note the exceptionally large vessels which are typical of climbing plants.

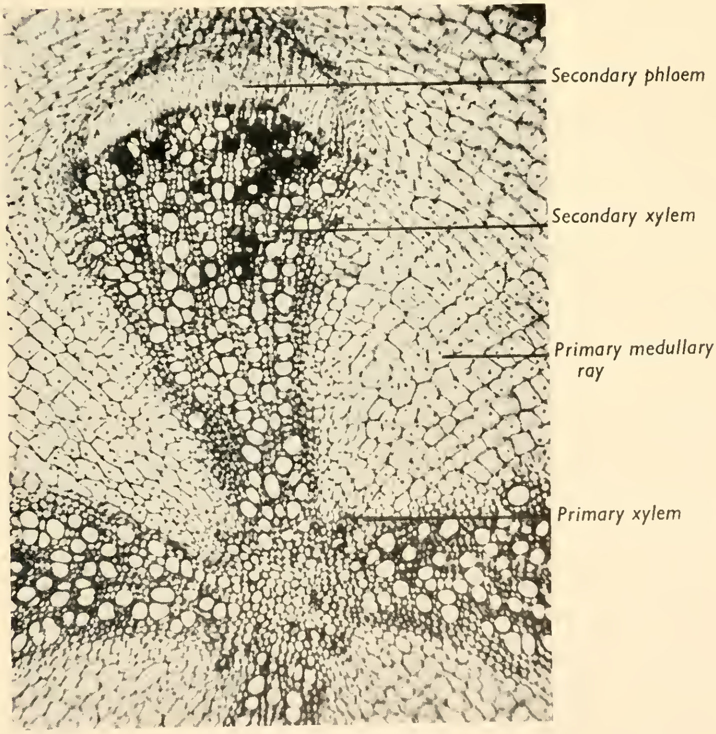

FIG. 804.—*Cimicifuga racemosa.* Transverse section of part of a tetrarch root showing secondary thickening with wide medullary rays.

It should be remembered that, whereas the primary xylems and phloems of the root are alternate, the secondary xylems and phloems lie on the same radii, with the cambium between them, which corresponds to the arrangement in the stem (Fig. 805).

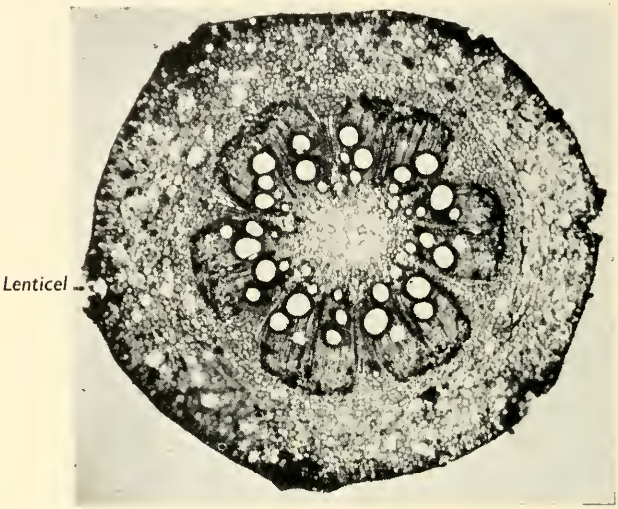

FIG. 805.—*Vitis quadrangularis.* Transverse section of a hexarch aerial root showing secondary thickening. Lenticels are present at the surface. Note the general resemblance to a stem.

PERIDERM.

When secondary thickening has begun, the expansion in diameter is rapid and the need for a new outer covering which is self-regenerating makes itself felt. Only a tissue capable of equally rapid expansion can keep pace with the growth of the cambium. This is provided by a second, independent cambium, which produces the new surface covering. The new cambium is called the **phellogen** or **cork cambium,** and the tissue it forms is the **phellem** or **cork.** Together they make up the **periderm.**

The pericycle, immediately outside the phloem, becomes the phellogen, by the rejuvenation of its cells. They divide repeatedly in the tangential direction, and at each division the outer cell becomes part of the cork, while the inner cell remains part of the phellogen, which is thus always one cell thick. As there are far more tangential than radial divisions, the cork cells are built up in regular rows, each row corresponding to one phellogen cell, and they soon form a very impervious covering. Naturally all the tissues external to the cork are cut off from their source of food supplies. They wither and die and are eventually shed. We shall discuss the nature and functions of cork more fully in the next chapter.

MODIFICATION OF ROOTS.

Many roots of peculiar form or function are known among Angiosperms, though very few occur in lower groups. These are all derivable from the normal type by the specialized development of one or other of its characteristic functions or structures, in a manner suitable to special circumstances.

When we speak of such structures as being "modifications," we imply that the simple type of absorbing root in the soil was the earliest type to be evolved and that the specialized forms have been derived from it.

(*a*) *Storage Roots.*

Among the simplest of these special cases are the **storage roots.** Normal roots usually store food reserves, but in some cases they are enlarged into **root tubers,** large, rounded structures with massive parenchyma tissues, packed with reserve materials. Sometimes the whole root is involved, as among soil-living Orchids, such as *Orchis morio* (Fig. 806); sometimes the base of the root thickens, as in the tubers of *Dahlia variabilis* (Fig. 807); sometimes small tubers are formed as branches on normal roots, as

FIG. 806.—*Orchis morio.* Plant showing storage root tubers.

in *Asparagus*. Frequently, as in *Oenanthe crocata*, these tubers are the means whereby the plant outlasts the winter season (Fig. 808).

Plants which belong to the so-called " root crops " are in a special category. Nearly all of these, such as the Carrot, Turnip, Beetroot, etc., are biennials (Fig. 809). In the first season the storage organ is formed, with only a very contracted stem which remains at soil level, bearing a group of large leaves. In the second season the stem elongates and bears flowers, drawing on the stored food below ground. The plant thus loses much of its food value to man, if it is allowed to flower or " bolt," as gardeners say.

Fig. 807.—*Dahlia variabilis*. Cluster of storage root tubers producing fibrous roots.

These storage organs are compound structures, the lower part being the true primary root, and the upper part being the hypocotyl of the seedling. The two parts are completely united into one organ. The nature of the storage tissue varies. In the Turnip and the Radish it is formed from parenchymatous secondary xylem. In Carrot and Parsnip it consists of parenchymatous tissue which chiefly represents secondary phloem and secondary cortex. In the Beetroot and Mangold it is largely soft xylem tissue in concentric rings, alternating with parenchymatous phloem. The rings are formed by a succession of short-lived cambia which are produced by the pericycle. The same structure occurs in many storage roots (Fig. 810).

FIG. 808.—*Oenanthe crocata.* Root tubers.

FIG. 809.—*Beta vulgaris* showing the swollen storage organ partly derived from the root and partly from the base of the stem.

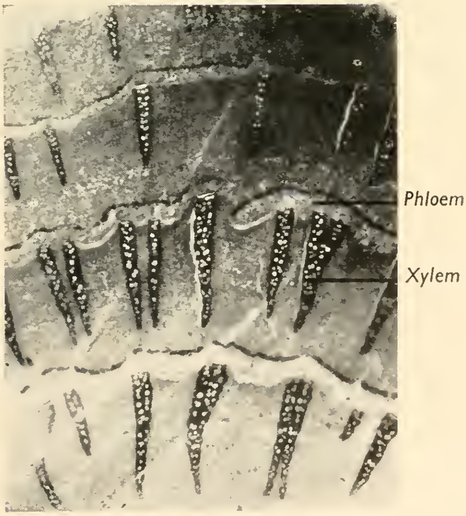

FIG. 810.—*Chondrodendron tomentosum.* Transverse section of the root showing concentric rings of vascular tissue which are only partly lignified.

(*b*) *Contractile Roots.*

A very interesting modification is shown by **contractile roots,** which are formed by many perennial herbaceous plants. The most striking examples are found on the bulbs and corms in Monocotyledons of the families Liliaceae and Iridaceae (Fig. 811). Perennial tap roots such as those of the Dandelion are also often contractile though to a lesser extent. These specialized roots are long, straight, thick and fleshy. In young plants of *Gladiolus* they may be thicker than the corm itself. They grow straight downwards, without branches or root hairs. They only last for two or three months and they contain at first abundant stores of glucose, which are rapidly consumed. As the reserves disappear, the cortex collapses in a series of transverse zones, which shortens the whole root by 30 to 40 per cent. This exercises a forceful pull upon the plant. In the case of bulbs and corms, where these roots are produced only at the close of the growth season, the plant is drawn bodily downwards and the yearly repetition of the process carries the plant down to a certain level, after which the formation of contractile roots ceases. If the bulb is then dug up and replanted near the surface, however, the process begins again.

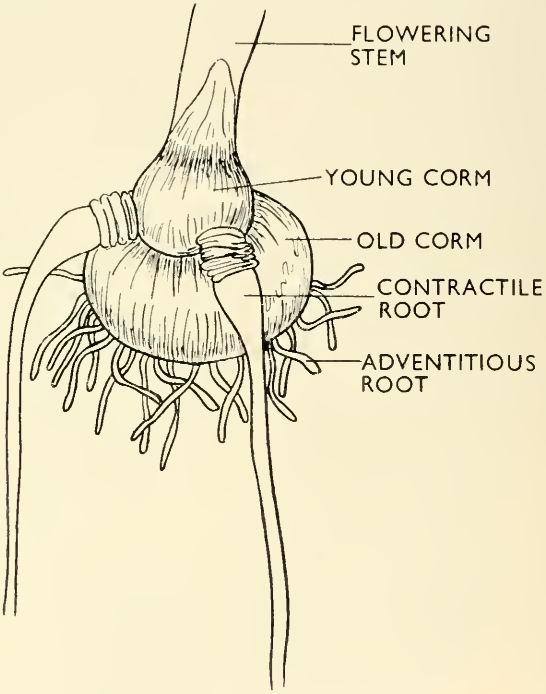

Fig. 811.—*Crocus sativus.* Corm with contractile roots. (*After Fritsch and Salisbury.*)

Contractile roots are also formed in some rhizomatous species such as *Polygonatum* and *Asparagus*, where no drawing of the plant downwards results and their function seems to be only that of giving more secure anchorage in the soil against the effects of wind on the large aerial shoots.

(*c*) *Buttress Roots.*

Many tropical trees show remarkable **buttress roots** around the base of the trunk. They are formed by the bases of the main roots, in which secondary thickening is unsymmetrical, being chiefly on the upper side. This results in the formation of thick, woody walls, running obliquely between the trunk and the ground (Fig. 812). They are sometimes so large that two men, standing one on each side of a buttress, would be hidden from each other. Some authors have suggested that this additional support of the trunk is rendered necessary by the great height of many tropical trees and perhaps by the prevalence of hurricane winds, but this is largely guesswork.

FIG. 812.—*Eriodendron anfractuosum.* Tree showing buttress roots with horizontal growth.
(From a photograph lent by the University of Florida, U.S.A.)

(*d*) *Horizontal Roots.*

A common habit among tropical trees is the production of roots which grow horizontally along the surface of the soil, spreading widely around the tree. Although they are a marked feature of tropical forests, it is not possible to say what advantage, if any, is gained by this method of growth.

(*e*) *Aerial Roots.*

Aerial roots are produced by most plants which grow as epiphytes (see Volume IV.). In many cases these roots may be of enormous length and of very rapid growth (4 to 6 in. per day). Roots of this kind are formed by many tropical Aroids and they hang down in large numbers, like cords, from the branches of the jungle trees, forming a remarkable feature of the forests (Fig. 813). When they reach the ground they penetrate the soil and produce a normal, branching root-system. Among epiphytic Orchids the aerial roots are, however, short and wholly aerial and hang loosely in the damp air of the jungle (Fig. 814). They can absorb rain and condensed moisture directly from the air. Such supplies of water are naturally intermittent, and the ordinary equipment of delicate root hairs would be quite unsuitable for an environment which is liable to periods of drought. Instead of a piliferous layer these roots are clad with a special tissue called **velamen,** which may be many cells thick (Fig. 815). The cells are dead and empty. Their walls are perforated with round apertures and are striated with ribs of cuticle. In fact the tissue is functionally a sponge, like the cortex of *Sphagnum*. On its inner side the velamen is bounded by a layer of cells with thickened walls, corresponding to the exodermis. When, as frequently happens, this layer

FIG. 813.—Aerial roots of epiphytic Aroids hanging from high trees in the tropical jungle. Alto da Serra, Sao Paulo, Brazil.

FIG. 814.—*Dendrobium sp.* Aerial roots of an epiphytic Orchid, covered with white velamen tissue.

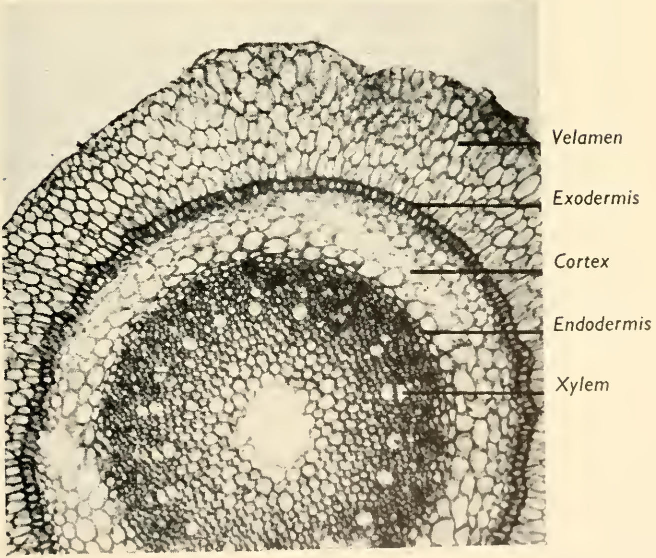

FIG. 815.—*Vanda teres.* Transverse section of an aerial root showing broad zone of velamen and thickened exodermis.

is highly thickened, there are unthickened "passage cells" produced at intervals, just as in the endodermis. As the velamen is external to the exodermis it must be a derivative of the dermatogen and is therefore analogous to the multiple epidermis often found on shoots and leaves.

The velamen is colourless and papery, so that from the outside the root looks dead, but the dead layer is also translucent and the cortex within is full of active chloroplasts to which light can penetrate. The obvious suitability of velamen to the conditions of epiphytic life has often caused it to be described as a choice example of "adaptation." Unfortunately for this idea, the tissue is not restricted to epiphytes. It is found also in many soil-rooting Orchids and in other Monocotyledons, *e.g.*, *Asparagus*, where no epiphytism exists. Needless to say, this does not detract from the usefulness of the velamen in the epiphytes which possess it, but it does point to another and probably more correct view than the adaptational one, namely, that the velamen is an anatomical peculiarity which has made possible the adoption of the epiphytic habit by plants which possessed it, though it has not obliged all of them to adopt epiphytism.

(*f*) *Pneumatophores*

Analogous to the epiphytic roots which hang in the air are those which grow up into the air from beneath the slime of tropical swamps, especially in the tidal swamp forests called Mangrove. These are known as **pneumatophores** or "breathing roots" (Fig. 816). They arise from long horizontal roots, and as they are negatively geotropic they grow vertically upwards, projecting eventually several inches into the air. They are usually only a few inches apart, so that very large numbers may surround a single plant, strongly recalling in appearance a crop of young Asparagus shoots. There

FIG. 816.—*Sonneratia alba.* Pneumatophores springing from underground roots around the trunk of an old tree. (*From Schmidt, in "Vegitationsbilder."*)

is a corky layer over each root, which covers even the apex, and the portion in the air bears numerous lenticels (see p. 867). Internally they possess an extremely spongy cortex, and in the cortex of some species there are also special cells, or idioblasts, which are empty and have thick cuticular ribs on their walls. Root hairs are not produced either by the pneumatophores themselves or by the horizontal roots from which they spring, but the pneumatophores form short absorbing branches from their lower portions and hairs are borne on these. Experiment has confirmed the old idea that pneumatophores serve as organs of aeration for the underground root system, buried as it is in tenacious mud with a low oxygen content. Diffusion into the horizontal roots is, however, limited to short distances. They are also centres of active respiration, and their vertical growth may be necessary to place the absorbing roots at the most favourable level. In sandy soils they are much fewer or may be absent.

The submerged roots of some swamp plants, such as *Jussieua* in warm countries, are surrounded by a greatly enlarged cortex called **aerenchyma,** which is formed of thin, dumb-bell shaped cells, with big intercellular spaces. Although this is submerged, its function is probably that of increasing the absorptive surface, not for water but for dissolved oxygen, which is in low supply in warm water.

(*g*) *Haustoria*

Parasites among the Flowering Plants make use of modified roots as a means of penetrating the tissues of the host plant. In *Orobanche*, the Broomrape, it is the primary root of the seedling which performs this function. It has no root cap and is the only root formed by the parasite, except some short exogenous outgrowths, which serve only for fresh attachments and may be modified roots. In *Lathraea*, the Toothwort, and in the green semi-parasites on grass roots, of which *Euphrasia*, the Eyebright, is an example, it is the branches from an otherwise normal root system which attack and penetrate the roots of the hosts (Fig. 817).

The Dodder, *Cuscuta*, has only a temporary root, in the seedling stage. The embryo has no leaves, and when the root has withered the thread-like stem grows independently on the surface soil for a short while, but perishes if it does not quickly find a host plant. Thereafter it twines around the stem of the host, like its relative, *Convolvulus*. Its nourishment is obtained by means of numerous penetrating suckers which spring from the surface of its stem nearest to the host. The resemblance of these suckers to the adventitious hold-fast roots of the Ivy has led to the general belief that they also are adventitious roots, specially modified. If so, they have been so far modified that it is difficult to find any root character which they possess. The stem of *Cuscuta* has four cortical layers. From the outer two there first develops a flat pad which attaches itself firmly to the epidermis of the host. In the centre of this pad, and involving all four cortical layers, there grows out a penetrating organ, the point of which is formed of elongated cells, which penetrates between the epidermal cells into the host cortex (Fig. 818). Here the long cells of the point take on independent growth and spread through the tissues. A strand of xylem and phloem now differentiates in the sucker and makes connection between the vascular tissues of the host and the corresponding tissues in the *Cuscuta*.

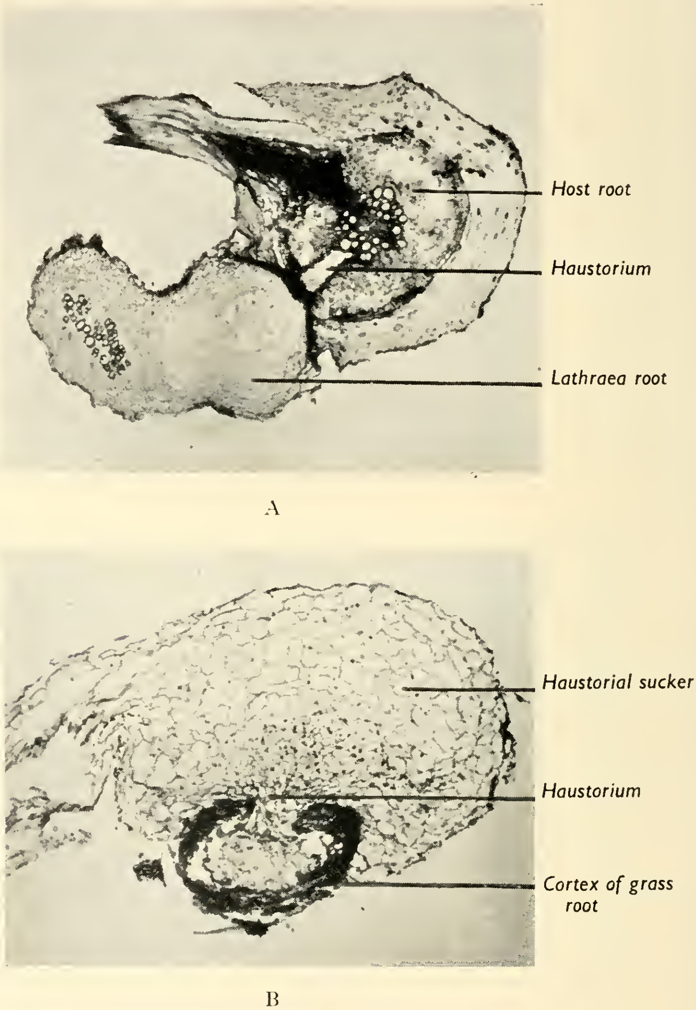

FIG. 817.—Haustorial roots of parasites. A, *Lathraea squamaria* (Toothwort) on Elm. B, *Pedicularis sylvatica* (Lousewort) on a grass root.

In all the above cases of parasitic attachments the vascular tissues of the host are the object of the attack, and substances are deflected from them into the parasite. It is difficult to find a common morphological basis for all such parasitic attachments, but they are sufficiently uniform in function to be grouped together biologically, and they are given the name of **haustoria.** The peculiar attachment organs of the Mistletoe will be reserved for treatment later (see Volume IV).

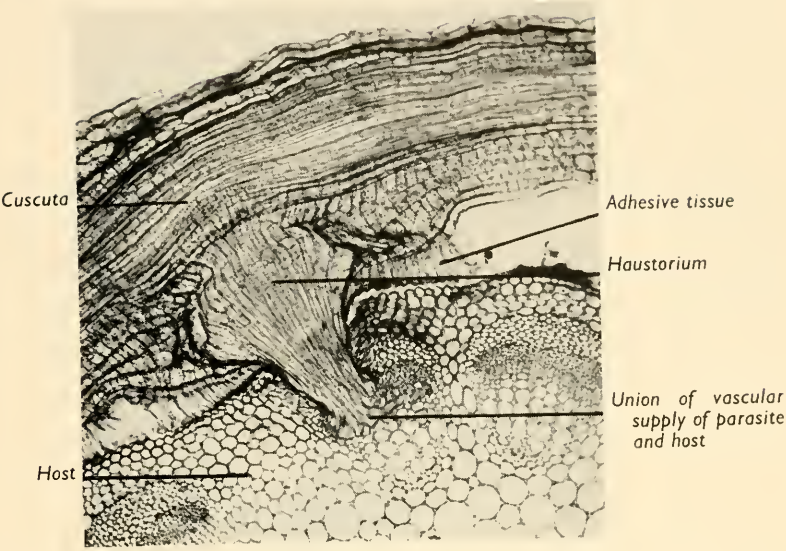

FIG. 818.—*Cuscuta epithymum* (Dodder). Transverse section of Clover stem, with parasitic stem cut longitudinally showing haustorium and adhesive pad.

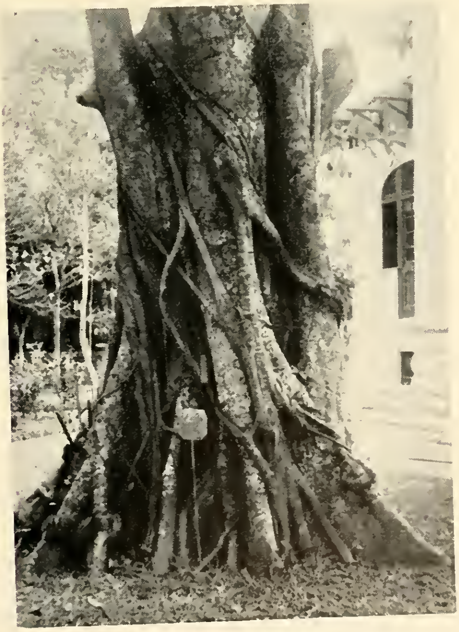

FIG. 819.—*Artocarpus integrifolia.* Trunk surrounded by the clasping roots of an epiphytic *Ficus.*

The foregoing modifications of the normal root in structure or function are for the most part shown by members of the primary root system. There are some further modifications which are characteristic of adventitious roots.

(*h*) *Climbing Roots*·

Many tropical climbers, especially of the family Araceae, make use of **clasping roots,** which are non-geotropic but respond negatively to light and are markedly sensitive to touch. These reactions cause them to cling closely to the bark of the supporting tree, which they envelop with a stout network (Fig. 819). Absorbing roots are produced separately in some cases. The latter grow directly downwards and eventually enter the soil. Both types are evidently modifications of one common root-form and differ from one another in little except in the larger vessels of the absorbing root and the thicker sclerenchyma of the clasping roots.

FIG. 820.—*Hedera helix* (Ivy). Shoot with adventitious climbing roots.

A similar modification is familiar in the common Ivy (*Hedera helix*). Adventitious roots are formed in great numbers on the side of the stem next to the support (Fig. 820). Normally these remain short and unbranched and become precociously corky. They attach themselves to the support by the formation of mucilage from the surface cells of the apex (Fig. 821). The

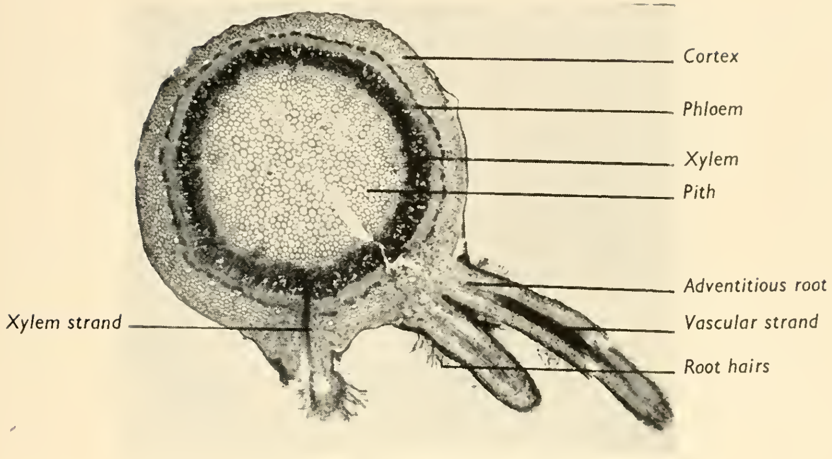

FIG. 821.—*Hedera helix.* Transverse section of stem showing climbing roots with root hairs.

free-hanging shoots do not as a rule produce holdfast roots. Apparently some moisture is necessary for typical holdfasts to develop, but if there is an excess of moisture or if they are grown in water they become normal roots. They may be regarded therefore as normal roots impeded in development by their conditions of growth.

FIG. 822.—*Zea mais* (Maize). Showing the origin of stilt roots from the basal nodes of the stem.

(*i*) *Stilt Roots*

Adventitious roots sometimes form supporting **stilts.** A good example is shown by the Maize, which develops a cluster of roots from the first one or two nodes above ground level (Fig. 822). They grow obliquely downwards into the soil and give added support to the stem, which, with its large leaves and heavy cobs, is very vulnerable to the effects of wind. Stilt roots are also well shown in *Pandanus*, (Figs. 823 and 824). Less familiar, but much more striking, are the stilt roots of the Mangroves. Several species of *Rhizophora*, *Sonneratia* and *Avicennia* make up the tidal woodlands in tropical bays and estuaries. All these trees are supported by scaffoldings of stilt roots, which may cover many square yards round each tree, making a formidable entanglement over the ground (Fig. 825). Not infrequently the base of the stem rots away, so that the tree is left perched on its stilts above the mud, like a giant vegetable crab.

(*j*) *Prop Roots*

Prop roots are those formed from the main branches of a tree. They grow straight downwards to the soil, which they enter and form underground branch roots. As they become thickened they give support to the branches, which are thus able to continue their horizontal growth, producing more prop roots at intervals. The best example of this is *Ficus benghalensis*, the Banyan Tree (Fig. 826). Banyan is the vernacular name for a merchant, and it was given to this tree because it was the customary shelter for itinerant pedlars, who set up stalls in their shade. Some of the biggest specimens have been used as shelters for whole villages of native huts.

(*k*) *Thorn Roots*

It only remains to mention two minor but curious modifications. The first is the formation of **thorn roots** at the base of the stem in several species of Palms. As in the case of stem thorns, these begin as normal structures but their tissues soon become densely sclerotic, including their apices, which then cease growth. In addition to root thorns, which are modifications of the roots themselves, some plants bear **root spines** which are outgrowths from the roots, *e.g.*, the Palm, *Iriartea exorhiza*, the big spiny stilt roots of which are used as graters in Panama.

(*l*) *Cortical Roots*

The second is the case of **internal** or **cortical roots** in several Monocotyledons, including especially *Tillandsia* (Fig. 827) and *Vellozia.* These roots grow directly downwards from their point of origin in the pericycle of the stem, penetrating the cortex as they go. Eventually they emerge from near the base. In *Vellozia*, which is common on exposed rocky places in south Brazil, these roots are not indeed truly internal. It is more correct to say that they actually make up a pseudo-cortex, covered and protected by a sheath of persistent leaf bases. The intensely dry habitat would no doubt prevent the growth of exposed aerial roots. A comparison suggests itself

FIG. 823.—*Pandanus leram.* Plant with numerous large stilt roots, hanging on a Mango tree.

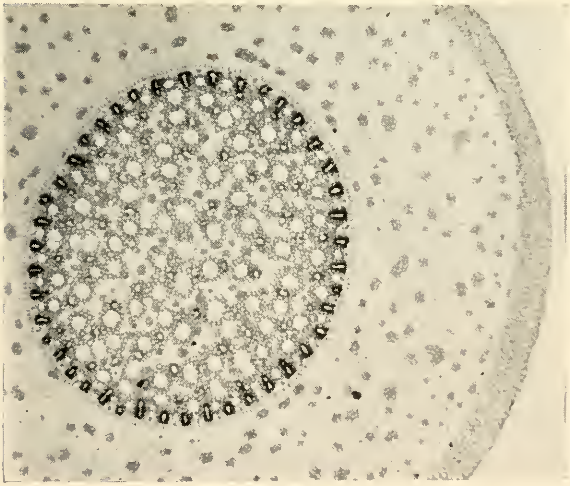

FIG. 824.—*Pandanus sp.* Transverse section of an aerial root showing very numerous xylem groups and abundant sclerenchyma strands.

FIG. 825.—*Rhizophora mucronata.* Entangled stilt roots in a Mangrove swamp.
(*From Wilson, "Plant Hunting," Stratford House, New York.*)

FIG. 826.—*Ficus benghalensis.* Development of prop roots from the horizontal branches. (*From Schimper, "Plant Geography."*)

with the compact mantle of roots which encloses the stem in the Tree Ferns and in their fossil relative *Psaronius.*

ROOT BUDS

One of the most fundamental characters of roots is that they bear no leaves, but they may and frequently do, in certain species, produce buds, which usually arise endogenously in the same manner as branch roots. Only in *Linaria* are the root buds exogenous. A few cases are known in which even the root apex may become transformed into a bud, namely in the Monocotyledons *Listera* and *Neottia* (Orchidaceae) and in *Anthurium* (Araceae).

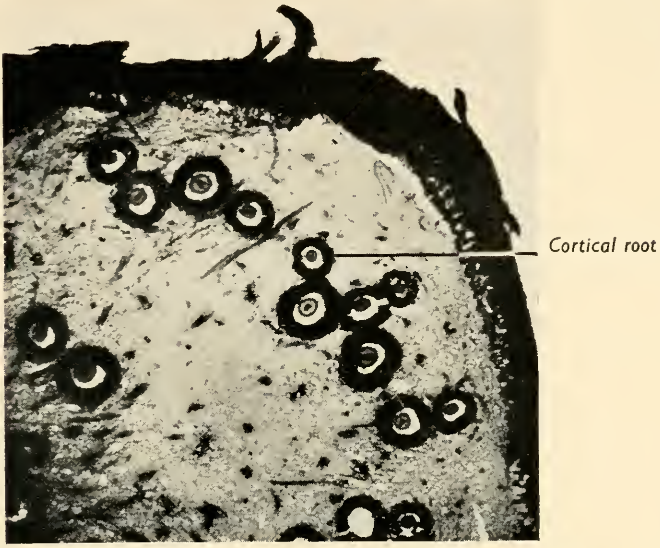

Fig. 827.—*Tillandsia recurvata.* Transverse section of stem showing numerous internal roots.

This formation of adventitious buds may be divided into three categories on biological grounds.

1. *Reparative.* Buds formed as a sequel to root injuries or to the destruction of the normal shoot system. This is common in woody plants and is often additional to the formation of buds of the next category. Among herbs there are fewer examples, and in most herbaceous plants where reparative buds are formed there are no others on the roots, *e.g.*, *Crambe*, *Cochlearia*, *Anchusa* and *Morisia*. They form a valuable means of vegetative propagation.

2. *Accessory.* Buds formed as part of the normal development in addition to the usual stem buds. They may serve as a means of vegetative propagation and are often called "suckers." They are common among woody plants, *e.g.*, *Populus*, *Rubus*, *Rhus*, *Prunus*, *Hydrangea*. They are rare among herbs. Well-known examples, however, are *Rumex acetosella* and *Epilobium angustifolium* and certain other aggressive weeds.

3. *Necessary.* These are buds which are the plant's only means of survival, normal buds being abortive or lacking. The saprophytes *Pyrola* and *Monotropa* are in this category and here also may be classed *Lepidium latifolium* and *Armoracia vulgaris* (Horse Radish) since they scarcely ever set good seed.

Linaria vulgaris (Toadflax) is a peculiar case. Not only are the root buds exogenous, but they appear in the seedling stage, and their growth replaces the main shoot, which aborts early. Some buds are also formed on the hypocotyl.

This leads us to the most peculiar case of all, that of the family Podostemaceae, whose members grow only in tropical waterfalls and exhibit the most surprising variety of forms, most of which are thalloid. In their vegetative parts they are utterly unlike Flowering Plants (Fig. 828).

FIG. 828.—*Dicraea stylosa.* Showing the thalloid development of an adventitious root bearing leaves and buds (*From Warming, in "Die Naturliche Pflanzenfamilien."*)

Their developmental histories are very various, but follow the general principle that the main shoot of the seedling is abortive and is replaced by the outgrowth of adventitious roots from the hypocotyl. These develop into the " thallus " and give rise to branch roots, to leafy shoots and to flowers. These roots are flattened and contain chlorophyll. They cling very closely to the submerged rock surfaces to which they are attached by root hairs and by short, exogenous outgrowths, called **haptera,** which resemble the holdfasts of the Ivy and serve the same purpose. In extreme cases the outgrowth from the hypocotyl has lost even the form of a root and develops into a circular crust on the rock, almost exactly like a Lichen. The shoots which arise from these "roots" are endogenous, but they can scarcely be called adventitious since they form part of the regular course of development. The family presents some of the most interesting phenomena of adaptation to environment in the whole plant world.

The Evolution of Roots

The possession of true roots is generally regarded as a distinguishing character of vascular plants, but as a matter of fact some traces of root formation can be found among the Bryophyta. A few species of Hepaticae and Musci have leafless, branched, downward extensions of their axes which it would be arbitrary to exclude from the category of roots since they correspond both in their general morphology and their functions with those of higher plants. There is indeed no reason why a gametophyte should not develop roots like a sporophyte. Among the lower Pteridophyta, in which the gametophyte and the young sporophyte are very much alike, it must have been an open question at one period of evolution which would become the rooted plant and the chief agent in the colonization of the land.

In the majority of the Spermatophyta the embryonic plant normally begins life with a main root which appears to be a downward prolongation of the main axis, and in the embryos of many Seed Plants the axis is a unitary structure with growing points at both ends, while in the tissues between one cannot distinguish the root and stem portions until a late stage of germination. This condition in the embryo has suggested that the primary root is simply a downward extension of the primary axis. If we look, however, at those members of the Thallophyta which normally grow attached to a substratum we see that the base of the axis terminates, not in a root, but in an attaching organ or holdfast. In comparing these lowly plants with the Spermatophyta we would gain the impression that the essential step in evolution which has produced the root was the establishment of a basal growing point, whereby the axis became bi-polar and acquired the power of extending in both directions. But we would get a false idea of this evolution if we were to imagine it as taking place in a fully evolved axis such as that we are familiar with in the Seed Plants. The evolution of the root took place among the lower Pteridophyta, and some of the lowest of that group, notably the Psilotales, are rootless even at the present day. The evolution of the root did not therefore coincide with the development of the land habit of life but occurred among plants which were already land-living. Nevertheless its importance is due to the conditions of land life, which restrict water absorption to the underground parts.

The lower end of the axis in the most primitive land plants—the "antiapex" as we may call it—did not form a root but a bulbous swelling, corresponding to the thallophytic holdfast, which was well developed in the fossil Psilophytales and perhaps survives among many of the Pteridophyta in the embryonic foot which attaches the young sporophyte to the gametophyte. This foot, not the primary root, is the true anti-apex of the embryo in such types. In the embryonic Lycopod the first root is normally a side growth, sometimes indeed arising close to or even actually at the stem apex. The anti-apical position of the primary root with which we are familiar in the Dicotyledons has only been reached in the higher plants in association with the enclosed embryo and the disappearance of the attaching foot.

Bower has called the young stages in the development of the Bryophyte embryo the " primitive spindle," the anti-apex of which is also a foot, not a root. The view here put forward is therefore in sharp contrast to that of Campbell, who traces the origin of the root to the meristematic base of the sporophyte in *Anthoceros*, on the assumption that the primary root is itself the anti-apex.

It seems much more probable that root and shoot have both alike been differentiated from the branches of a dichotomous body like the rhizome of *Psilotum*. The close resemblance of this rhizome to the prothallus stamps it as essentially primitive, though it already shows a differentiation into branches which produce leafy shoots, and branches which remain underground, a mode of differentiation which strongly suggests the origin of the root system from specialized branches of a rhizome (Fig. 829). If this be so we would conclude that a condition in which there are many lateral roots is more primitive than one in which there is a single, anti-apical root. It is interesting therefore to note that von Goebel maintains, on different grounds, the same position. He calls the Pteridophyte type, which lacks an anti-apical root, **homorhizal,** and the more advanced type, with opposed root and shoot poles, **allorhizal.** To arrive at the latter condition the many dichotomies of the rhizome, such as that of *Psilotum*, have apparently been reduced to one, occurring in the early divisions of the embryo. The divergence to the extreme of 180° of the two axial poles thus produced may be put down to the advantages secured by this divergence, in view of their opposed biological functions (see Fig. 628, D).

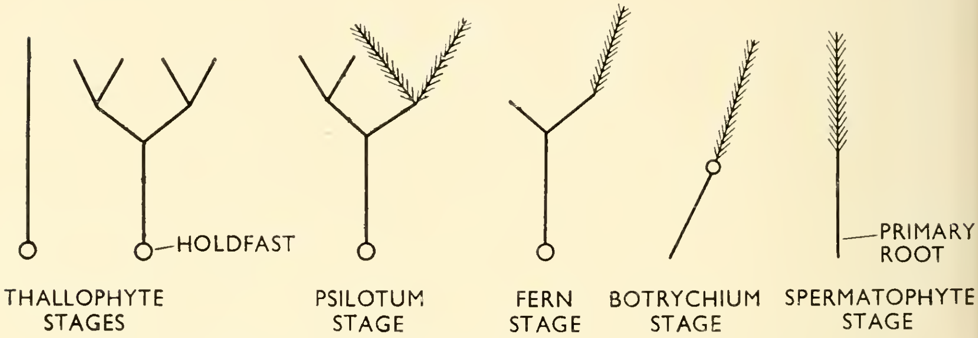

FIG. 829.—Diagram to illustrate the theory that root and shoot are two differentiated positions of a primitive dichotomous thallus.

This suggestion of the origin of roots obviously leaves to be explained much that we consider typical of roots, especially their endogenous branching and the presence of a root cap. It is worth remark, however, (1) that the primary root itself is not endogenous and that lateral roots are not invariably so, notably in the primitive Lycopods, both living and extinct; (2) that the formation of roots is restricted in the more primitive vascular plants to the base of the leafy shoots; and (3) that many instances are known of roots without a root cap.

Examples of the absence from roots of every individual one of the so-called typical characters can indeed be quoted, except, perhaps significantly, that of leaflessness. Under the concept of their origin here put forward this is only to be expected, since leaflessness would be a basic character common to all branches alike, in the primitive dichotomous body. It could be argued that it is the presence of leaves on the aerial stem, not their absence from the root, which is the acquired character.

CHAPTER XXI

THE ANGIOSPERMAE: STEMS

In the stem of the Angiosperms we have to do with a structure of so protean a nature, so far surpassing the root in the manifold diversities of its form and structure, that we are brought at the very beginning against a fundamental morphological difficulty : How are we to define the stem ? The only all-embracing answer is : " The stem is that organ which bears the leaves." This definition, although correct so far as it goes, reveals the bankruptcy of the old system of morphological categories, for it tells us nothing of the nature of the stem itself, which it describes only in relation to another morphological concept, namely the leaf, and it is based upon function, not upon structure.

This difficulty has impressed morphologists for more than a hundred years past and has given rise to a variety of theories, which we may group under the general name of **phytonism,** having the common aim of supplanting the idea of the stem as a distinct morphological entity. Morphologists are still, in fact, pretty sharply divided into those who support this idea and those who do not.

The old idea formed by the purely descriptive outlook of systematists was that plants consisted of three ultimately distinct categories of organs, each a true unity, namely Rhizome * (root), Caulome (stem) and Phyllome (leaf), each capable of great variation yet each remaining true to its essential nature. This was first challenged by C. F. Wolff (1759), who maintained that the stem is formed of a bundle of united leaf stalks, prolonged downwards, so that in cutting across an old stem one is really sectioning a mass of leaf traces. This is the prototype of a number of later theories, all based upon the longitudinal segmentation of the stem. Opposed to them are several rival schemes which treat the stem as transversely segmented into a sympodium of units, generally called Anaphytes, each corresponding more or less closely to a single internode with its attached leaf or leaves and their axillary buds.

We have previously shown (p. 650) that Zimmermann has proposed an analogous view of the elementary morphology of the shoot in which the primitively equivalent segments are called **telomes,** some fertile, that is to say, spore-producing, and some sterile, evolved from the fertile segments. From these, through the " overtopping " process, all the organs of the higher plant may have been evolved.

It may be pointed out that most of these theories are purely logical constructions and that, except in the last case, little or no attempt has been

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* This use of the term Rhizome must not be confused with the modern application of the term to an underground stem.

made to relate them to known evolutionary facts. We have sufficiently expressed our views on this aspect of the subject in Chapter I.

In the great majority of plants the leaf-bearing axis and the leaves collectively constitute the **shoot.** In the preceding Chapter on Roots we referred to certain cases of rootless plants. Analogous cases occur of plants in which the axis is lost. For example, the seedling of *Streptocarpus* begins with the normal dicotyledonous form. One cotyledon and the stem apex rapidly abort, and in some species the hypocotyl also, while nothing more develops except an adventitious inflorescence from the base of the single cotyledon, which itself becomes the sole foliage leaf.

The case of the Duckweed (*Lemna*) is still more extreme (Fig. 830). The entire plant consists of minute floating segments which proliferate by budding from their edges. Whether these segments should be classed as leaves or stems has been much discussed, although, as we have seen above, there is reason to believe that the distinction is one of name only. Comparison with the nearest related genus *Pistia*, however, confirms the view that they are equivalent to leaves and thus that the plant has no axis.

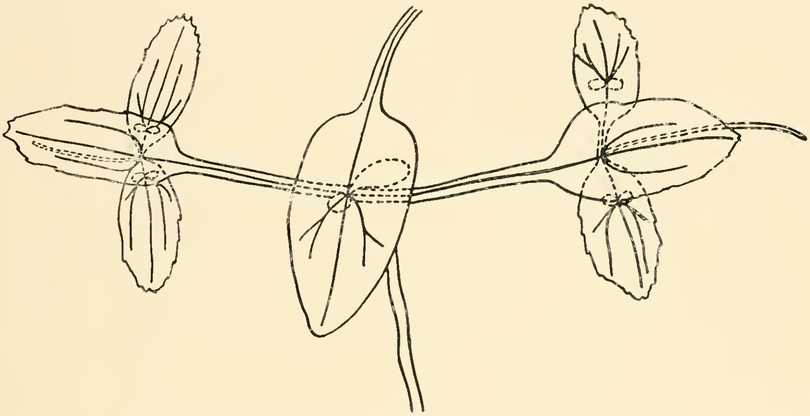

FIG. 830.—*Lemna trisulca.* Floating plant showing proliferation by budding from the segments. (*After Goebel.*)

The principal function of a normal stem is unquestionably that of displaying the leaves, and there are scarcely any stems, however much altered from the normal form, which do not bear leaves of some sort, although they may be reduced in certain cases. The possession of leaves or leaf scales may indeed be regarded as the most definite distinguishing character of a stem.

In addition to supporting leaves the stem must also provide channels of supply for the movement of fluids both to and from the leaves, and the internal anatomy of the stem is suited to this function. Stems also serve a number of subsidiary functions, though not in all cases. These are, briefly: (1) Storage, either of food materials, or of water, or both. (2) Associated with this is the function of perennation, that is, of tiding the plant over the season of winter rest. (3) Propagation or vegetative spreading. (4) Climbing. (5) Photosynthesis, especially in cases where the leaves are short-lived or reduced.

Variation associated with these functions leads to that great diversity of form or habit, which is one of the most striking features of plant life.

From the earliest times men have distinguished trees, shrubs and herbs, and the distinction persisted even in scientific classification until the eighteenth century. We shall deal with the classification of " Life Forms " in Volume IV. Here we need only mention the distinction of habit which divides plants into **perennials, biennials** and **annuals.**

Perennials may be woody, either tree-like with one main trunk, or else shrub-like with a cluster of stems. They may also be herbaceous, dying down to the ground level each winter and persisting only by underground organs.

The duration of perennials is very variable and depends to some extent on their rate of attaining flowering maturity. Some herbaceous plants live only five to six years. Large trees, on the other hand, may take twenty-five to thirty years to reach the flowering stage. The common factor in all perennials is that they are **polycarpic,** that is to say, they flower and fruit repeatedly.

The age and size that trees may attain is not definitely limited. The following are a few famous examples :—

Eucalyptus amygdalina. Australia. Height, 470 ft. Diameter at base, 33 ft. Age, about 4,000 years.

Adansonia digitata. Africa. Diameter at base, 33 ft. Age about 5,000 years.

Quercus pedunculata. England. Diameter at base, 13·5 ft. Age about 1,500 years.

Castanea sativa. Sicily. Diameter at base, 66 ft. Age about 700 years.

Nevertheless trees are not immortal and there are historical records of the apparently natural death of very old trees.

Biennial plants last only for two years. In the first season they produce at soil level a very contracted stem which bears a rosette of leaves. During the second season the stem elongates and bears the flowers and fruit, after which the whole plant dies.

Annuals complete their whole life, from seed to fruit, in one year or less, in some cases even in a few weeks, *e.g., Senecio vulgaris* (Groundsel), so that several generations may be passed through in one summer, while nothing but the seeds remains alive through the winter. Biennials and annuals are therefore typically **monocarpic,** fruiting but once.

Exceptions, however, occur. If an annual is prevented from ripening its seed it may not die but may survive and flower again in a second or even a third season. Certain monocotyledonous perennials, on the other hand, are naturally monocarpic. Many species of Bamboo flower simultaneously every twenty to thirty years and then die, leaving only seed to carry on the race. The " Century Plant," *Agave americana*, reputed to flower only after

100 years, does in fact wait for upwards of half a century before sending up its 50-ft. inflorescence, and thereafter dies. Perhaps the most striking case is that of the Talipot Palm, *Corypha umbraculifera*, which grows to a height of over 60 ft. in about thirty years, without flowering (Fig. 831). The terminal inflorescence, when it is eventually produced, may be upwards of 40 ft. high and nearly as much across, being in fact the largest known. As soon as the seeds are ripe the whole tree dies forthwith. In all these cases it seems to be the exhaustion of the food reserves demanded by the large masses of flowers which kills the plant.

FIG. 831.—*Corypha umbraculifera* (Talipot Palm).
Plant in flower.
(*From Kerner, "The Natural History of Plants," Blackie & Sons Ltd.*)

Cases have also been recorded of trees, even such great trees as the Spanish Mahogany, producing monocarpic seedlings which flowered and died without growing beyond the seedling stage. Many other similar departures from the normal show that life habit is far from being fixed and unchangeable.

Morphology of Stems.

It is often said that a leading character of stems is the formation of joints or **nodes,** at which the leaves are attached, separated by varying lengths called **internodes.**

While this is generally true of the Dicotyledons, it is often otherwise among Monocotyledons, where the broad-based leaves are set so closely in succession that no distinction of nodes is possible. In fact, as we shall see later, this is the primitive condition which we find in the buds of most plants, at the growing points where the leaves are developing. The separation of any pair of leaves by the elongation of the stem between them is only accomplished slowly and is closely dependent upon the growth and vigour of the leaves themselves.

If we examine a straight, well-developed shoot of a plant with opposite leaves, such as that of a Willow Herb, we see that the leaves near the base are small and that the internodes are correspondingly short. The latter increase in length regularly to the level at which the leaves have reached their maximum size and from there they decrease again, in association with immature leaves, until they merge into the apical bud, where they are hidden by the closely placed leaf primordia. On a long shoot, with many leaves fully mature, there will be a corresponding length of stem in which the internode length is roughly constant. It is evident that the growth in length of each internode is to a large extent determined by the nourishment which the leaf immediately above it can supply. In the branches of trees the same sequence of varying lengths of internode occurs independently in each year's growth, beginning at the level of the terminal bud of the previous year, so that each year's growth may be regarded as a distinct " shoot generation."

The case we first mentioned with opposite leaves is the simplest and clearest in this respect. Where the leaves are single and spirally arranged matters are more complex, for in such stems the internodes overlap and their growth is a composite of effects due to several of the leaves above. This will become clear when apical growth has been studied.

Although the length of internodes appears to be closely associated with leaf development and does not continue after the leaf has reached full size, it is otherwise with growth in thickness. This is a continuous process, and the diameter of the stem will be found to increase regularly, downwards, as far as the level of the cotyledons, without direct relation to leaf growth. It continues even after the growth in length of the stem as a whole has ceased and in the older parts of the stem, which no longer bear leaves.

The foregoing is a particular example of what are called **symmetry relationships** in the plant. The longitudinal symmetry which we have just considered is based upon an imaginary line joining the main stem apex to the main root apex, *i.e.*, the **longitudinal axis,** which is the chief constructional line in the architecture of the plant and which we may therefore consider as its principal and probably its oldest dimension. Its outstanding character is its **polarity,** that is to say, its possession of two opposite and different poles, at the stem apex and the root apex respectively, which are permanent and are replaced if destroyed.

Lateral symmetry relationships are classified under three headings :—

1. *Radial Symmetry*, when a part is organised equally on all radii round the longitudinal axis.
2. *Bilateral Symmetry*, when a part has two distinct sides, *i.e.*, is not organised equally on all radii round its axis. If both sides are alike it is called Isobilateral, or if they are unlike it is called Anisobilateral.
3. *Dorsiventral Symmetry*, when a bilateral part has two differently organized faces, *i.e.*, possesses a distinct top and bottom or back and front.

Radial organs are also, for the most part, **orthotropic,** that is, vertically placed, while bilateral and dorsiventral organs are mostly **plagiotropic,** that is, horizontal or inclined in position.

This latter distinction points to the fact that symmetry is not entirely a matter of inner organization, but, as has been shown by many experiments, can be fairly easily modified by external influences, especially by light and gravity, which are the factors most affected by differences in the position of an organ. For example, many bilateral shoots, such as those of the flattened Cactus, *Opuntia*, develop with radial symmetry in the dark and the bilateral side shoots of *Tradescantia* become radially symmetrical, like the main axes, if grown free from gravitational effects on a klinostat. The dorsiventral internal structure of many leaves can be changed into an equifacial structure by development under conditions of equal illumination of both surfaces, and the anisobilateral growth of some leaves, like those of the Elm in which one half is bigger than the other, can be reduced to equality by severing the vascular supply to the larger side.

Such experiments show that symmetry is frequently the imprint of growth conditions, but these conditions operate upon nutritional differences, growth tendencies and "correlations," that is, influences due to the effect of one growing part upon others, which arise from internal causes quite independently of external influences and which vary greatly in the degree to which they are susceptible of external control. The more fundamental such inner tendencies are, which probably means the older they are, the more difficult they are to change. Thus it is practically impossible to change the bipolarity of the axis or to change a bilateral leaf into a radial structure by experimental means, though even such fundamental changes have sometimes occurred during the vast and prolonged course of evolution.

BRANCHING OF THE STEM

Only a minority of Angiosperms have a single axis. The normal habit is for shoots, like roots, to multiply themselves by branching, which makes possible the division of functions between different branches and, above all, enables the leaves to be disposed to the greatest advantage. The amount of branching is inversely related to the size of the leaves. Unbranched plants have either large leaves, *e.g.*, Palms, or no leaves at all, *e.g.*, Cacti.

Theoretically the simplest way of branching is by the division of the apical growing point into two. This method, known as Dichotomy, is not uncommon among lower groups, and occurs also in some Angiospermic roots, but is very rare in stems, the only definite examples being in two Palms, *Hyphaene thebaica* and *Chamaedorea martiana.* The former is common in North Africa and shows very marked dichotomy, with an angle-leaf at the stem junctions, as in *Selaginella.*

The normal method of branching is **axillary,** that is, from buds which arise in the **leaf axil,** *i.e.*, the angle between leaf and stem. Axillary branches are said to be subtended by the related leaf. Every axillary bud resembles the apical bud in structure and has a similar power of growth by the elongation of its internodes. Axillary buds seldom commence developing immediately they are formed. There is commonly a resting period before unfolding begins, which may, however, be only a few days in an annual. In woody perennials the buds formed in one season do not generally grow until the following year, and they may remain dormant indefinitely. This, as we shall see in Volume IV., is conditioned by the physiological dominance of the apical bud. In all cases where this bud retains permanently its capacity for active growth, the branches which develop from axillary buds remain lateral and subordinate to the main axis, and this is called **monopodial branching** (Fig. 832), *e.g.*, *Acer platanoides.*

Neither the main axis nor the branches have, however, always the power of unlimited growth. Frequently the apical bud is transformed into a flower or flowers, which, being themselves of limited growth, close its career. Again, in some of our common trees, notably the Elm and the Lime, the tip of each young branch dies back to a node during the summer and drops off, leaving a small round scar to mark the place. Whatever may be the fate of the terminal bud, the effect of its disappearance is to leave subsequent growth to the axillary shoots. This is called **sympodial branching** (Fig. 833).

In trees or shrubs with opposite leaves the uppermost pair of axillary buds may develop next season with equal vigour and hence arises a semblance of dichotomy to which we have referred above. Where the leaves are set singly, however, as in the Elm and the Lime, there is only one bud at the node to which the shoot dies back, and its subsequent growth carries on the axis in the original line, so that an appearance of monopodial growth is preserved. The same appearance of monopodial growth in a sympodial system may also be seen where a terminal flower is pushed to one side by the growth of the nearest axillary bud, which continues the line of growth of the main axis. When the shoots of a tree end in flowers, as in the Horse Chestnut, the branching may be monopodial for some years, until the flowering stage is reached, and then becomes sympodial.

The sympodial method, by which the responsibility for active growth is regularly passed on from branch to branch, permits a degree of specialization

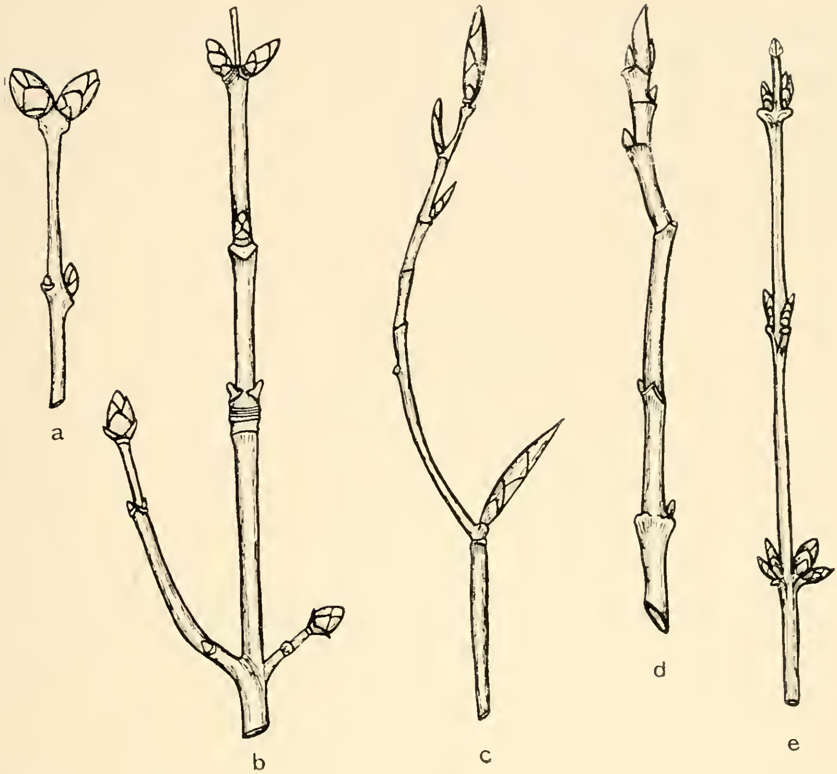

FIG. 832.—Types of branching. A, *Syringa vulgaris* (Lilac) sympodial. B, *Acer pseudoplatanus* (Sycamore) monopodial. C, *Fagus sylvatica* (Beech) monopodial. D, *Magnolia lennei* monopodial. E, *Forsythia intermedia* monopodial with serial buds in the leaf axils.

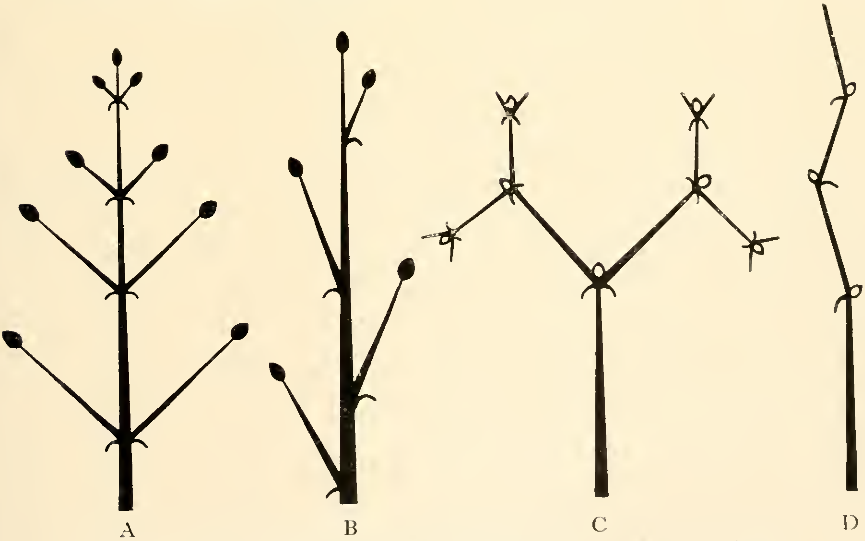

FIG. 833.—Types of branching. Monopodial types: A, *Acer*; B, *Fagus*. Sympodial types: C, *Syringa*; D, *Ulmus*.

for particular biological purposes, whereby certain branches of limited growth may be modified in structure to a degree that is rarely possible with the monopodial system. We shall deal with a number of such biologically specialized branches at the end of this chapter, when we shall see that the majority are the products of sympodial branching. To put it less teleologically we may say that the biological specialization of a branch in most cases limits its growth and makes sympodial branching inevitable.

The distinction between " long " and " short " shoots, that is, between those which are indefinite or unlimited and those which are definite or limited in growth, is thus usually a question of the specialization of the short shoot for some other purpose than that of growth, but the distinction is not always sharp or fixed and transitions and reversions occur. An important case is that of the reproductive shoots. Specialization for reproduction is usually associated with limited growth, and in the case of the flower this specialization has gone so far that it is rare indeed for the axis of a flower to resume indefinite growth. When it does so, the flower is said to be " proliferating."

Even those branches which are nominally unlimited in growth may differ in their rates of growth. Most frequently, in woody plants such as trees, the buds near the top of last year's growth form the longest branches, and the length of branch produced by each bud decreases regularly downward to the base of that section of the shoot. The lowest branches on each year's growth may remain permanently dwarf and form the reproductive shoots, *i.e.*, the flowering and fruiting " spurs," which are so important in fruit trees (Fig. 834). In most cases, *e.g.*, Apple and Pear, the growth of these spurs is sympodial, but in the Plum it is monopodial.

The angles at which branches are borne are very variable between species, but are relatively constant within the species. Spreading branches are described as **patent,** those which lie close to the main axis are called **fastigiate,** and an alteration in this character may mark a distinctive variety, as in the fastigiate Lombardy Poplar (*Populus nigra*, var. *italica*) in which the branches all tend to be vertical.

Branches which make a wide angle with the vertical, *i.e.*, plagiotropic branches, frequently assume a dorsiventral symmetry through the horizontal placing of leaves and of side shoots, or by a marked difference in the size of the leaves on the upper and lower sides of the branch respectively. Although this has a direct physiological meaning, in that it ensures the best exposure of the leaves to light, yet this symmetrical character is often permanently fixed in the organization of the branch. If such plagiotropic branches are removed and used as cuttings for propagation, the dorsiventral habit is often retained and a plagiotropic plant is the result.

Branches are classified under different orders. Thus the primary vegetative axis and all equivalent branches from it belong to the first order ; flowering shoots belong to the second order, and the flowers themselves to a third order. If the primary axis is an underground structure then the leafy shoots above ground become branches of the second order and so on. Four orders is the maximum number, so far as is known, and the majority of plants have only two or three orders. Like most other classifications this must not be applied too literally, for there are many cases where the distinctions are obscure.

Reference was made above to the dropping of the terminal portions of young shoots in Lime and Elm. In Poplar and Oak a similar shedding of branches, called **cladoptosis,** occurs on a larger scale. Numbers of small branches are dropped every year and inspection shows that they are usually those devoted to the production of male flowers. As these twigs have no leaves except at the apex, they grow very little and therefore fail to maintain a firm union with the growing tissues of the trunk. The outward pressure of these expanding tissues soon breaks the insecure connection of the twig and it falls.

FIG. 834.—*Pyrus malus.* A three-year-old flowering spur with terminal cyme of flowers.

An analogous fate befalls the dead twigs which are often left on the lower and inner parts of large trees. These twigs, being unfavourably placed, have so little power of growth that their water supply is drained away by the competitive demands of higher and more vigorous shoots. Once dead they have no further power of maintaining their union with the growing tissues of the parent branch, and they are broken off by its continued expansion. Their stumps get buried in the wood of the growing trunk and appear as knots when the wood is cut up for use.

The axillary buds, upon which branching depends, arise from the superficial tissues of the main growing point, and are thus **exogenous.** The bud rudiment arises immediately above a leaf rudiment and exactly on the same radius (Fig. 835). That is to say, that buds are invariably median in the axil of the subtending leaf. Except in the flowering shoots of some plants the appearance of a bud rudiment always follows the appearance of a leaf rudiment, and extra-axillary buds are never formed at the apex. Some variation, however, exists in the relationship of the bud and the leaf. The bud may sometimes appear on the surface of the axis, or in other cases it may be formed from the actual base of the leaf. No special morphological significance need be attached to such variation in itself, but it has interesting morphological consequences. Later growth may intervene to separate the bud considerably from its point of origin. When the bud stands on the stem it may thus be carried upwards on the internode, indeed the whole elongation of the internode sometimes occurs between the bud and its leaf axil, so that the bud seems to lie just below the node above. From this circumstance arise the numerous cases of the so-called adhesion of branches to their parent axis or of branches or flowers arising from points other than the axil of a leaf. All such cases can be traced to the displacement of axillary buds.

FIG. 835.—*Acer pseudoplatanus.* Winter buds.

When, however, the bud stands on the leaf base the subsequent growth of the latter may lead to the appearance of shoots or flowers arising from a point on the surface of the leaf, a circumstance extremely puzzling to older morphologists, who regarded the leaf as an organ fundamentally different from the shoot.

The opposite case may also occur when the bud, or the zone of tissue on which it stands, elongates before the leaf has fully developed. Then the leaf appears to be attached to the axillary branch which it actually subtends.

All these peculiarities arise from the phenomenon of **intercalary growth,** that is, growth in length which occurs in any part of a plant away from the growing point itself and therefore not part of the main growth system which centres there.

In general, it may be said that whichever organ of the pair, leaf and axillary bud, originates first will develop first. Normally this is the leaf, and in many cases the appearance of the bud rudiment in its axil may be delayed until the node is some distance from the apical meristem zone, so that the bud meristem seems to be secondary, that is to say, it has no direct connection with the apical meristem. The reverse, namely, the earlier development of the bud rudiment, occurs chiefly in flowering shoots, where the leaf subtending the flower may have a very limited power of growth, or may be entirely abortive, so that the flowers (as in many Cruciferae) appear to have no subtending leaf at all.

The precocious development of axillary buds may also occur in vegetative shoots, a well-known example being *Berberis*, in which the leaves of the long shoots are transformed into spines, and in their axils stand rosettes of true leaves, the precociously developed leaves of the axillary shoots, which are not due to elongate into branches until the following season.

The suppression of bud growth, on the other hand, is usually associated with late appearance. It often happens in the axillary buds themselves that the enveloping scales, which are modified leaves, develop no axillary buds of their own until the bud begins to grow, which may be a year after its formation. These buds are very small and have little power of growth. When the axillary branch has grown, some of these buds are left at its base, where they remain dormant so long as the branch continues its growth. Eventually they are submerged by the expansion of the main stem, and they may remain, embedded but alive, long after the axillary branch which bore them has disappeared. Every old tree carries hundreds of such hidden buds. Should any catastrophe befall the active portion of the tree, the diversion of food materials to these buds starts them growing and they emerge as the vigorous " stool shoots " which may spring out like a thicket from the stump of a tree which has been felled or from the trunk of a tree which has been lopped of its branches.

Considerable differences may be observed between the vigour of growth of different branches, which are usually due to differences in the amount of food available, whether by the accident of favourable position or the availability of stored reserves. In the short shoots, with their closely set leaves, the movement of foodstuffs elaborated by the leaves seems to be less free than in the long shoots, with the result that they become loaded with carbohydrate reserves. This seems to encourage flower formation, and in many plants, especially fruit trees, it is noticeable that flowering is usually confined to the dwarf branches or " spurs." The aim of a cultivator is to encourage the production of spurs over the greatest possible length of stem, and this he does by judicious pruning. In the summer he removes the upper third of each young shoot. This diverts nutriment to the lower buds. Of these a few of the uppermost will start to grow into leafy shoots, but those at the base will receive only enough to encourage them to dwarf growth. When winter comes he cuts the shoot back nearly to the uppermost of these spur growths, leaving a top bud to continue next year the growth of the branch, while the spurs flower and bear fruit. Thus the whole branch system can be kept " furnished," as it is called, with spurs, whereas in trees that have been left alone there will be lengths of stem in which the buds have not received enough nourishment to grow at all and have remained dormant.

Some growers practise the Lorette method of pruning, cutting the summer shoots down in July to $\frac{1}{4}$ in. from the base. The theory is that the basal buds, which were themselves formed in the axils of bud scales, when stimulated to growth will only have enough vigour to produce spurs, so that a cluster of spurs will be formed. Opinions differ as to the success of the method in this country, though in France it is very popular.

More than one bud may be formed in a single axil, though it is exceptional. Series of two or three buds are not uncommon and as many as ten may be found. They form a succession in age and size. In Dicotyledons the series is always vertical, with either the oldest or the youngest at the bottom, while in Monocotyledons the series is always lateral, with the oldest bud in the middle. Either branch or flower buds may be involved or both together. The suggestion that this multiplicity of buds is due to the precocious branching of one axillary bud, is probably correct in some instances, though in others the buds seem to be formed independently at the stem apex.

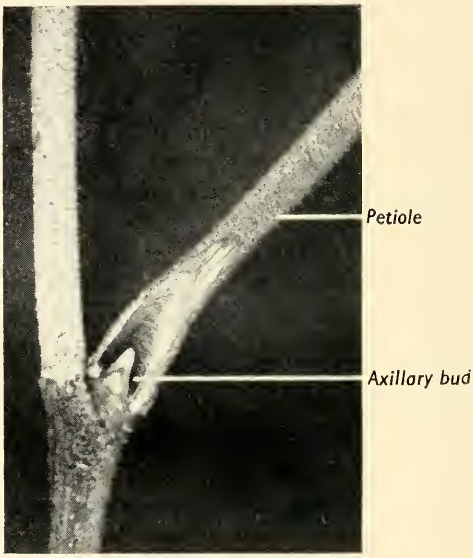

FIG. 836.—*Platanus orientalis*. Section through the base of a petiole showing the enclosed axillary bud.

A good many trees and shrubs, especially in the Tropics, protect their axillary buds by structural arrangements. Two striking examples among well-known plants are the Plane, *Platanus orientalis*, and the Locust Tree, *Robinia pseudacacia*. The axillary buds in both cases are enclosed by the growth of the base of the leaf stalk and are only exposed in winter when the leaves fall (Fig. 836). In the second species there are three buds in series, of which only the lower pair are enclosed, while the top bud is left free to grow into a temporary branch which is replaced next season by a permanent branch from the upper of the two protected buds.

That the axillary position gives, in all cases, valuable protection to the bud is no doubt one reason for the universal adoption of this arrangement in the Angiosperms. The relationship between bud and leaf is, however, physiological as well as morphological, and as the nutrition of the bud must depend largely upon the neighbouring leaf, this is readily understandable. It is well known that the presence of the leaf has a repressive effect on the growth of its axillary bud, at least in woody perennials, where the postponement of bud development may be biologically important. This fact comes out in the behaviour of cuttings, in which the removal of a leaf may be the condition necessary to ensure the growth of its axillary bud.

The interesting experiments of Dostal with the Enchanter's Nightshade (*Circaea lutetiana*) show that the effect of the leaf on the growth of the bud may be qualitative as well as quantitative. He took cuttings from various heights on the stem. Each piece, including a node with a pair of opposite leaves, was split lengthwise, and the leaf was removed from one half only. From the pieces with leaves the buds developed as follows: from the lowest nodes, as plagiotropic stolons; from those higher up, as plagiotropic branches which later became vertical; and from the upper nodes as vertical flowering shoots. From the leafless pieces, however, the buds grew into vertical leafy shoots at all levels.

Truly adventitious branches, that is to say, branches produced abnormally without relation to axillary buds, are very rare on angiospermic stems, though they are not uncommon on leaves. The few cases recorded are from the hypocotyls of seedlings. They may also develop from wound callus, as we shall describe later in this chapter. Most of the apparently adventitious branches arise from dormant buds buried in the bark, as we have already described. These buds were originally exogenous so that the branches formed from them are also truly exogenous. Endogenous branching of Angiosperms is practically unknown. An exception must be made for the flower shoots which grow from the main trunk, *i.e.*, in the "cauliflorous" trees of the Tropics. There is evidence that these may arise from the pericycle, like the endogenous branches of roots.

Before leaving the important subject of branching we should glance at the special case of unbranched plants. They may be either primitively unbranched as in the Palms, or have assumed this habit by reduction from a branched type, as in the tiny uniaxial Mousetail (*Myosurus*). In practically all cases the habit is associated with large leaves, large, at any rate, relative to the size of the plant, so that a small number of them suffice for its nutrition The habit is commonly associated with very large or massive plants. It has been called "megaphytism," and is attributed by Cotton to the possession of a giant apical meristem which exerts a highly repressive influence, owing to the amount of auxin which it produces, on the growth of all axillary buds.

Apical Growth and Meristems

We have seen above that plant growth may be either apical or intercalary. The latter is, however, except in rare instances (leaves of *Welwitschia*) only temporary, while apical growth is conterminous with the life of the plant and may be in fact continuous in a uniformly favourable climate. This concentration of growth into a small, permanently embryonic area is one of the great differences between plants and animals. In a young animal growth is general and goes on until a specific size is reached, which is not widely different between individuals ; at this stage general growth ceases and we say that the animal is mature. A plant, however, is never mature in this sense. Apical growth persists as long as the plant lives, so that the size reached by a given individual is conditioned only by its age and its environment.

When we examine the apex of any growing shoot we see that it is occupied by a cluster of young leaves, the outer of which more or less closely enfold the inner. This is the **apical bud.** If growth for the year has ceased the bud will be encased, not with young leaves but with hard scales. This is a **winter bud,** which will remain dormant until next season. By the time winter comes the rudiments of next year's leaves will have been formed within the scaly covering, ready for rapid development in the spring. Some plants, especially trees, have all the leaves for the season thus prepared before the season begins (*e.g.*, Horse Chestnut), and even where this is not the case few of them continue to produce new leaves after June. They then form bud scales, within whose protective covering the preparation of leaves for the following season continues until October or November.

If we dissect a bud in either the active or the dormant state we see that the young leaves get progressively smaller as we go inwards, becoming finally microscopic at the centre. If we now examine microscopically a median longitudinal section of such a bud, we see that at the centre lies the true apex of the stem, a more or less dome-shaped mass of small cells, on the flanks of which the leaf rudiments arise successively as small protuberances. This is the **growing point** or **punctum vegetationis,** and the tissue of which it is composed constitutes the **apical meristem** (Fig. 837).

This polar concentration of growth at the apices of stems and roots is a very striking feature of plant organization. To trace its origin we should probably have to go back to the primitive cell-filament from which the axial structure of higher plants has been evolved, but there is little doubt that it is an expression of a polarity which is inherent in every part, indeed in every cell of the plant body. Each cell has physiologically a top and a bottom, a front and a back, a right side and a left, and though we can see nothing to suggest this in a normal tissue cell, it may come out clearly during the regeneration of tissues after a surgical operation.

Whatever its origin, let the fact suffice us that here in the apex are produced, from the meristem cells, all the organs of the plant. The process of their development we call their **ontogeny,** and the conditions of their ontogeny

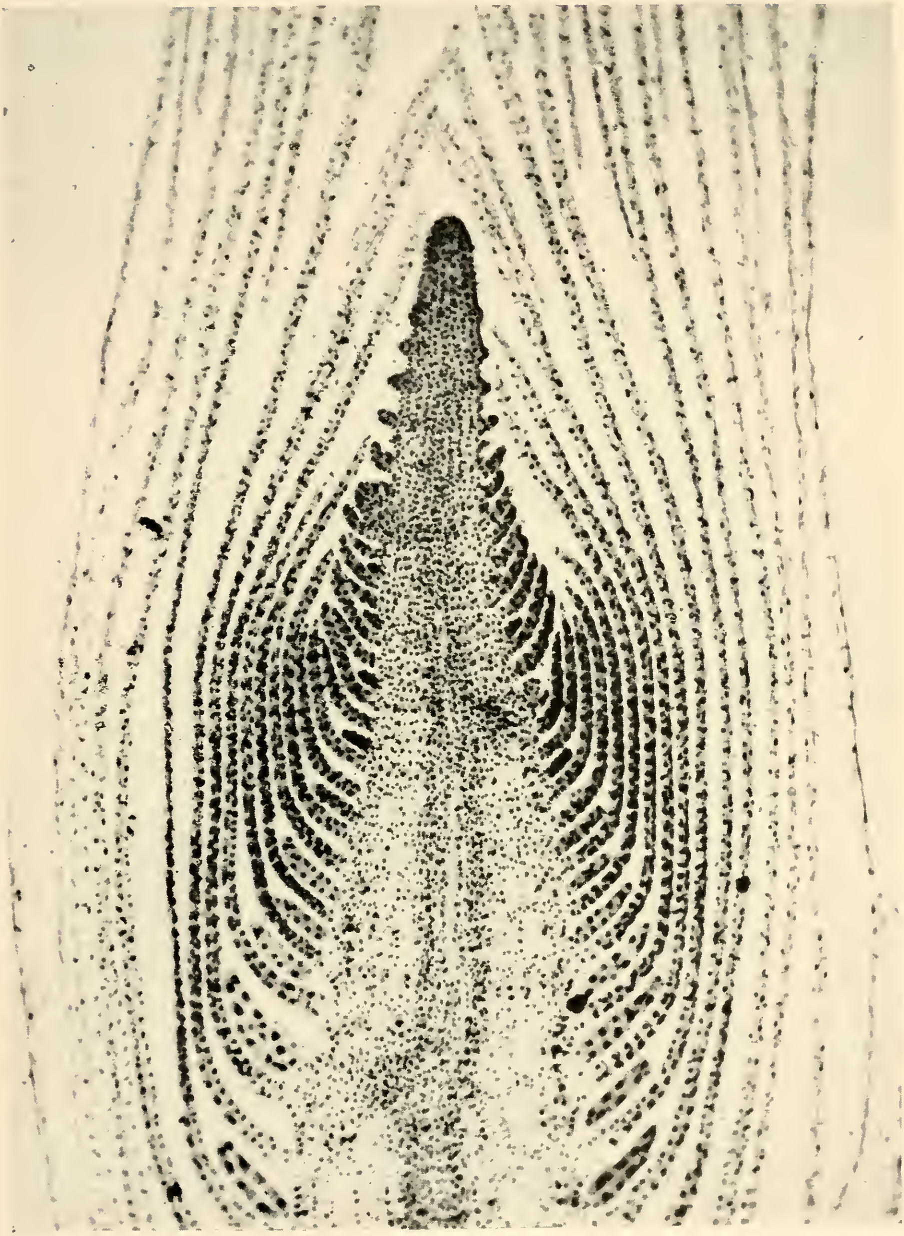

FIG. 837.—*Hippuris vulgaris.* Longitudinal section through the apical meristem of a leafy shoot showing the growing point and the origin of the leaf rudiments, which as they grow enfold the growing point in an apical bud.

have an extensive determining influence over all those features of the mature organs which, taken together, mark every species with its distinctive character.

There are two main categories of tissue in a plant, the **formative** and the **permanent.** They are complementary in function, for while the formative produce the permanent tissues, the latter nourish the former. Functionally the formative tissues are for growth and differentiation and the permanent tissues for assimilation and distribution. The meristem is therefore not simply one among many types of tissue in the plant, it is itself equivalent to all the types of permanent tissue together.

The name meristem means the divisible tissue, and its outstanding character is that of rapid and repeated cell division. The majority of meristematic cells only keep this character temporarily and soon pass into one or other of the paths of differentiation which lead towards the permanent tissues, yet, paradoxically, the meristem as such is permanent. There is in every meristem a terminal group of cells which never differentiate, but, like queen bees, produce the cells which do. This is the **initial meristem,** the source of all the rest (Figs. 838 and 839). The respective rates of growth and of differentiation are autonomously determined in the meristem itself and are so balanced that the meristem neither increases nor decreases in amount over long periods.

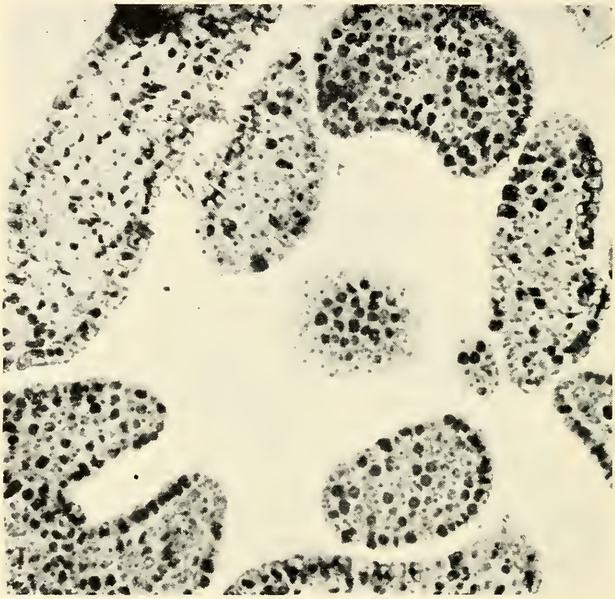

Fig. 838.—*Abutilon megapotamicum.* Dicotyledon. Transverse section through the apical bud showing in the centre the growing point of the stem surrounded by successive leaf rudiments.

The initial meristem is only a part of the formative tissues at the apex. Between it and the permanent tissues there is an intermediate region of derivative cells, which are not yet permanent in character and retain the meristematic quality of repeated division.

The apical meristem is thus not uniform in its nature. The initial meristem alone is completely undetermined, while the determination of the destiny of its products begins while they are still part of the meristematic tissue as a whole.

A cell which is destined for differentiation into permanent tissue retains the meristematic character for some time and may at first be indistinguishable from one of the initial cells, repeated division taking place, as shown by the frequency of mitotic figures.

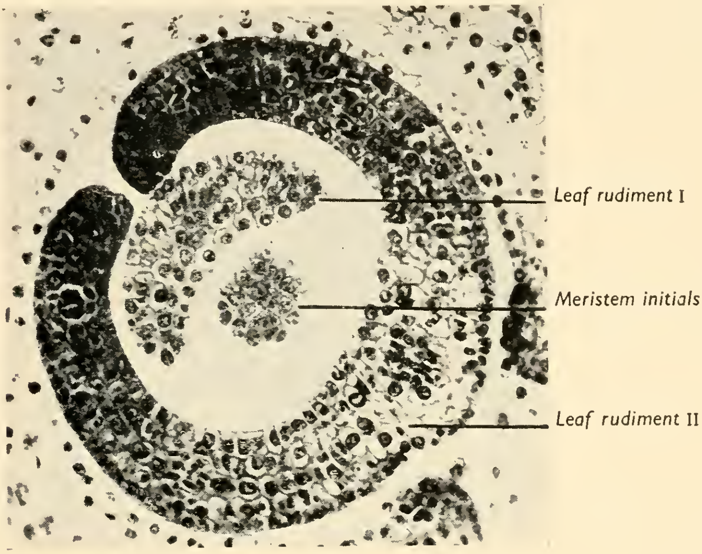

FIG. 836.—*Zebrina pendula.* Monocotyledon. Transverse section of the apical bud showing in the centre the growing point of the stem surrounded by two leaf rudiments. Note the rapid lateral extension of the leaf rudiments characteristic of Monocotyledons.

Physiological changes are taking place, however. Protein synthesis, which is characteristic of the meristematic state, is giving place to carbohydrate synthesis, and the accumulation of osmotically active sugars is probably responsible for the growth of cell vacuoles, the first visible evidence of change. The cell wall also changes, becoming thicker and passing through a highly hydrated stage, known as the amyloid stage, in which it is extensible but not elastic. This stage is very transient, but while it lasts the internal turgor pressure in the vacuoles causes the cell to enlarge considerably, with further enlargement of the vacuoles, which may now unite to occupy the whole central part of the cell. This is the phase of maximum growth. The cells become rounded off and small intercellular spaces appear between them, which are at first full of watery sap, but later contain air. These spaces form an inter-connected system between the cells, by means of which air can permeate all the inner tissues. Up to this point cell division still occurs but afterwards gradually ceases.

The process of change is not quite continuous. Two or three pauses in the process of enlargement, associated with maxima of cell division, may occur before division stops. The vacuolated but still expanding tissue should be classed as the **sub-meristem.**

With the entry of air into the intercellular spaces the cell wall loses some water and becomes more rigid, so that further expansion is resisted. The intercellular substance is also changing into the middle lamella, consisting of insoluble Calcium pectate and soaps, and the cells are more firmly bound together. Rapid growth ceases and the cell enters the phase of internal development which changes it into one or other of the types of permanent tissue cells.

These phase relationships may be summarized thus :—

First Phase.	Second Phase.	Third Phase.	Fourth Phase.
Initial Meristem.	Sub-meristem.	Cell Expansion.	Cell Differentiation.
Growth uniform.	Growth increasing.	Growth increasing.	Growth ceasing.
Rapid division.	Division rate falling.	Division rate falling.	Division ceasing.
No vacuoles.	Vacuoles appear.	Vacuoles enlarging and uniting.	Vacuolization complete.

During the above time-sequence there have also been spatial changes, for the activity of the initial meristem is unceasing and each differentiating cell is left further and further behind by the advance of the growing point. Indeed the inseparability of the ideas of space and time is nowhere better displayed than in organismal development.

We must now return to consider the initial meristem and its behaviour. The characteristics of the meristem cell have been described in Chapter XIII. We may recall here that each cell is a unit of semi-liquid protoplasm, enclosed in a thin and highly plastic wall ; that each cell is endowed with powers of active chemical synthesis and is therefore expansible, but is held in check by mutual pressure against its neighbouring cells. Growth and division rates among these cells are so balanced that they are all very similar in size and in appearance. Close examination shows, however, that in the initial meristem the surface layer of cells and one or two layers below it form distinct strata, in which all cell divisions are at right angles to the surface, *i.e.*, anticlinal. These layers therefore grow only in area or extent, but not in thickness, and each cell layer remains distinct. This region is called the **tunica.** It is characterized by its two-dimensional growth. Below the tunica lies a mass of irregular cells without definite arrangement, in which divisions occur in all planes and growth is therefore three-dimensional. This is called the

corpus (Fig. 840). Let us emphasize that these names are not substitutes for the three germinal layers of Hanstein which were described in the root. They are not morphologically determined but are distinguished simply by their mode of growth. Little is known as yet about the comparative organisation of the apex in different Angiosperms, but it is evident that there is great variability, and that the tunica, for example, may be from one to four layers deep. There is evidence that the various cell layers of the tunica and the cell mass of the corpus have a good deal of physiological independence. They seem to arise from a small number of separate initial cells, and the contribution which the different layers make to the permanent tissue is probably very variable. Certainly the outermost layer produces the epidermis and is directly continuous with it. The whole plant thus lies enclosed in a cell layer which can be traced back to the first periclinal divisions of the embryo, and its outer surface wall is in fact the enormously extended wall of the original oosphere, which surrounds the plant like an amnion. The leaf primordia are probably in most cases the product of the tunica layers only, but this cannot be definitely asserted.

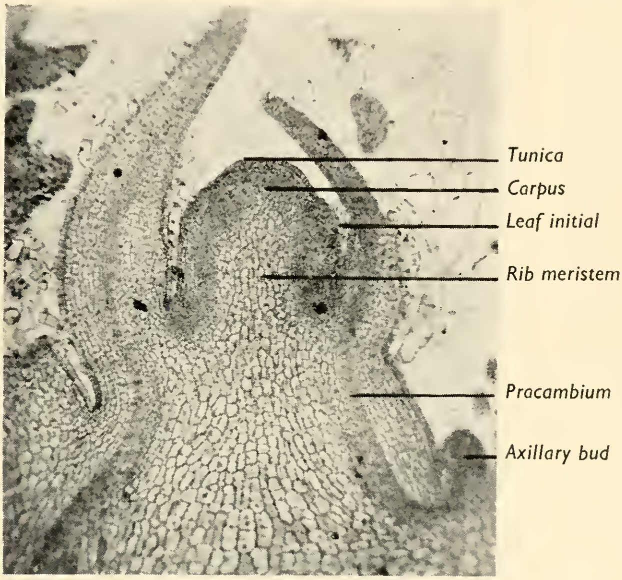

FIG. 840.—*Solanum tuberosum.* Longitudinal section of the apical meristem showing tunica and corpus.

The origin of these leaf primordia seems to be largely the mechanical result of combining area-growth in the tunica and volume-growth in the corpus. The balance between the two is maintained for a period by re-adjustment of the cells in their relative positions, which probably includes some sliding of cells against each other and changes in their shape, but eventually the increase of surface leads to the appearance of a fold on the flank of the apical dome (Fig. 841). This is a **leaf rudiment.** Once formed its further development follows a very orderly sequence of cell divisions in new directions.

The growth of the apex as a whole is therefore rhythmical rather than uniform. It proceeds by a succession of maximal and minimal areas. When the surface has expanded to its maximum area a leaf-fold is formed and the minimal area is regained. Each phase of this rhythm, the period from the initiation of one leaf primordium to the next is called a **plastochron** or unit of developmental time, which corresponds spatially to the interval between successive nodes.

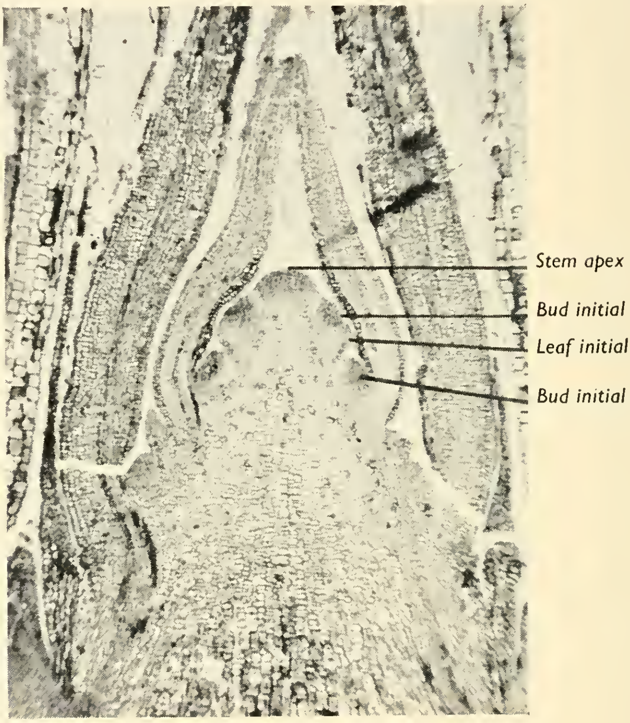

FIG. 841.—*Viburnum fragrans.* Longitudinal section of the apical meristem showing the sequence of leaf initials and origin of the axillary bud initials from the meristem.

Of course it must be realized that these few mechanical notions provide only the barest bones of an account of development at the apex. There must exist an immense complex of growth controls which determine the details in the development of organs, every one of which has a character peculiar to its species. This has led to the apex being compared to an " organizer," a somewhat mystical conception borrowed from animal embryology, which may only mean that the apex is a nodal point in a framework of chemical and physical gradients in the tissues, which by their interaction determine the place, direction, rate and time of growth in all parts and therefore control the development of the specific form of the plant.

The extent of and the relationships between the tissue zones at the apex reflect the direction and distribution of growth, which we can detect by the direction of the cell walls. Divisions are more frequent on the sides and at the base of the corpus than they are in the centre, and the sides may contribute to the peripheral tissues, while the base builds only the pith. The morphogenetic functions of the zones are, however, undoubtedly variable.

Below the corpus there is a well-marked transitional zone, called the **rib meristem,** where growth is mainly longitudinal and each cell divides transversely several times in succession, producing short vertical files of cells, surrounded by older, thicker walls and traversed by young walls. This tissue passes over gradually into typical parenchymatous pith by the equalization of the wall thickness and the expansion of the cells and readjustment of their relative positions. Elongation seems to be the chief change in all the submeristematic cells, conditioned partly by the resistance to transverse expansion exercised by the slower growing surface tissues and partly by the pattern of the thread-like molecules in the cell walls, which grow by longitudinal additions. Cells destined for vascular elements often elongate very precociously, even in the meristem, as if their cells were abnormally plastic, an effect attributed by some to the diffusion of auxin from the meristem. As we shall see in Volume III this diffusion is known to occur, while the effect of auxins in increasing the plasticity of cell walls is well known. Variation in the concentration of auxins at different points may therefore have important results in controlling the differentiation of tissues and the theory demands further investigation.

All this elongation of cells affects the spacing of the rudimentary leaves. They are pushed apart by the lengthening of the internodes and no longer overlap their neighbours, but assume the spacing and position of mature leaves. The length of an internode depends much more on the number of its cells than upon variations in cell size, and it is a general rule of growth that the longer active cell-division persists the larger is the resulting organ.

Differentiation of Tissues

The apical region of the stem is essentially a dynamic and highly plastic organization, and the developments that arise from it follow paths which are highly variable between species. During the past hundred years it has been the aim of research to discover the laws of this development and to bring some order into our ideas respecting it, but these efforts have not been highly successful. A superfluity of descriptive terms have been coined and they have been used in different senses by so many different authors that confusion has abounded instead of clarity.

The attempt to apply rigid definitions to the protean appearances in the differentiation of tissues has led, for example, to such absurdities as the inclusion of the protoxylem, in some cases, among " secondary " structures.

We must, however, adhere for descriptive purposes to some system of terminology, and though the following account does not pretend to finality it appears to agree with the facts so far as they are known.

In the great majority of apices there is to be found, below the apical meristem, a ring-like zone of meristematic tissue, which is delimited outwards by the vacuolization of the cells of the cortex and inwards by those of the pith. This forms a tubular downward extension of meristem which is called the **meristematic ring,** or sometimes, but less happily, the **residual meristem.** From this ring the vascular tissues are derived. The relation of the meristem ring to the apical meristem is variable, but it seems to come in most cases from the outer zone of the corpus.

The next development is that of the **procambium.** In a few cases the whole ring becomes procambium, and in such cases a continuous ring of vascular tissues is formed from the beginning, as, for example, in *Vinca.* In the majority of plants, however, the formation of procambium is localized at certain points on the ring, so that a number of separate vascular strands is formed. The cells of procambium are longer and narrower than those of the meristem and they become increasingly vacuolated. They are polygonal in transverse section and arranged at random. Cell divisions are mostly longitudinal, but they are not in a definite order, and the vascular elements derived from them are therefore not in an orderly arrangement either. The procambium is the same tissue as that called desmogen by some authors (Fig. 842).

Procambium becomes true **cambium** when its successive divisions become predominantly tangential, so that its cells and those of the derived tissues are arranged in radial rows. The cambial cells also become characteristically flattened as seen in transverse section. This is held to mark the beginning of the phase known as **secondary thickening.** When it happens that there is no procambium and orderly tangential division begins in the meristem ring, then obviously there is no distinction between primary and secondary structures. The change from one to the other must in any case be gradual and it is impossible to draw a clear line between them. It may be marked, even in the permanent tissues, by no more than some alteration in the character of the xylem elements, for example, by the exclusive formation of pitted vessels and the increase of fibre cells. Even when cambium has been established, the length of its cells and the length of the corresponding tracheids formed increase steadily for some years. The terms " primary " and " secondary " in plant anatomy imply therefore no more than a succession in time, not an opposition of character.

Where the development of procambium and consequently of vascular tissue is limited to certain points on the meristematic ring, the separate groups of xylem and phloem thus produced are called **vascular bundles.** When they begin to form they are still separated by unchanged tracts of the meristem ring, for which there are two alternative possibilities. They may become parenchyma, forming the **primary medullary rays,** or they also may develop, somewhat more slowly, into procambium and eventually into cambium, known as the **interfascicular cambium.** Even where parenchymatous rays have been formed they may later be bridged by a cambial band, linking together the bundle cambia, which is formed by regression (*i.e.*, de-differentiation) of parenchyma cells. The first type of interfascicular cambium, that which arises directly from the meristem ring, may form interfascicular zones of xylem and phloem, connecting together the vascular tissues of the bundles. On the other hand, the second type of interfascicular cambium, which arises from parenchyma may, and usually does, form nothing but more parenchyma, continuing outwards the primary medullary rays, so that the bundles remain permanently isolated. The former condition is characteristic of the truly woody trees and shrubs, the latter condition includes many woody climbers, such as the Vine.

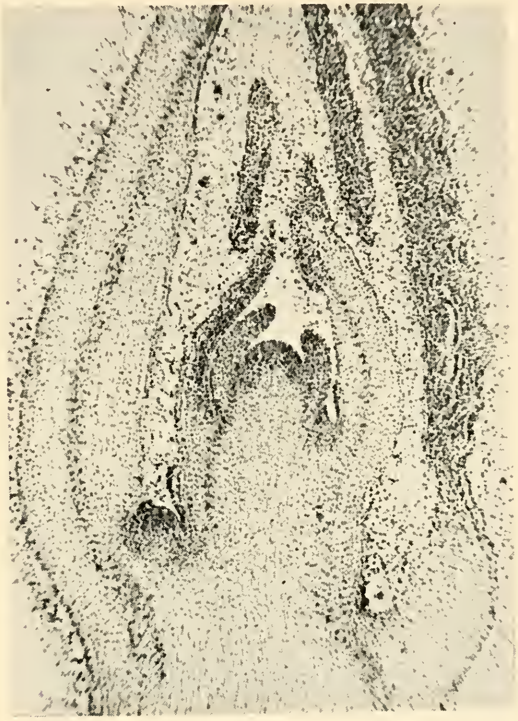

FIG. 842.—*Solanum crispum.* Longitudinal section of the stem apex showing the development of procambial strands in connection with the leaf rudiments.

The true herbaceous plant has no interfascicular cambium, and in the most reduced cases no cambium at all, the bundles being formed entirely from procambium, which originates in separate strands directly from the apical meristem, without even the formation of a meristem ring.

The scheme on page 856 summarizes these complicated relationships.

TYPES OF VASCULAR DIFFERENTIATION. (*After Esau.*)

Apical meristem

- Meristematic ring formed.
  - Continuous procambial ring.
    - Continuous primary vascular ring.
      - Continuous secondary vascular ring, *e.g.*, *Veronica*, *Vinca*, *Rubia*, etc.
  - Separate procambial strands with residual meristem between
    - Separate primary vascular strands
      - Interfascicular cambium directly from residual meristem. Continuous secondary vascular ring, *e.g.*, woody Dicotyledons, including woody herbs like *Helianthus*.
      - Residual meristem forms parenchyma. Secondary vascular strands remain separate.
        - Interfascicular cambium from parenchyma, produces primary ray cells only, *e.g.*, *Vitis*, etc.
        - No interfascicular cambium formed, *e.g.*, Herb type, as *Impatiens*, etc.
- No meristematic ring. Separate procambial strands from the first.
  - No secondary vascular strands. Extreme herb type, *e.g.*, *Ranunculus* and herbaceous Monocotyledons.

Each procambial strand originates in very close proximity to the base of a leaf primordium or actually in contact with its cells, and the strand in the stem is continuous with that which develops in the primordium itself. Every vascular bundle of the stem is thus a part of the vascular supply to a leaf, or, in other words, is a **leaf trace,** and is so from the procambial stage onwards. In other words, the vasculation in the stem does not belong to the axis *per se*, but to the leaves. Abnormal exceptions do not invalidate this general rule.

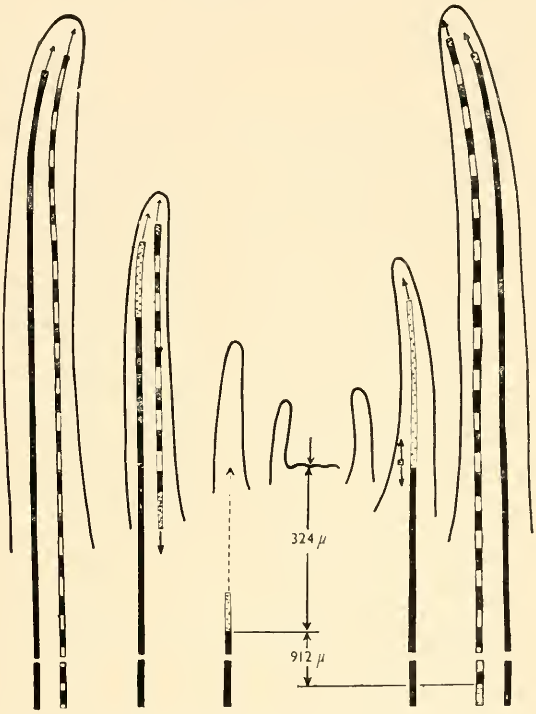

Fig. 843.—Diagram of the course of vascular differentiation at the apex of a stem of *Nicotiana*. Procambium stippled; xylem black and white; phloem black. The arrows indicate the direction in which differentiation is taking place. (*After Esau.*)

Although procambial connection between stem and leaf exists from the very beginning of the leaf, the development of vascular cells in the procambium does not begin until three or four plastochrons later (Fig. 843). Phloem development begins first. The first sieve tube makes its appearance at the outer edge of the procambial strand and is from the first connected in linear sequence with those in the older part below it. The differentiation of this sequence of sieve tube units progresses slowly upwards into the leaf, but it does not, as a rule, reach quite to the apex of the leaf, where sieve tubes may be absent even at maturity.

The first xylem element, normally a spiral tracheid, appears at the inner edge of the procambium. It lies close to the base of the leaf primordium into which the strand of procambium runs, and it is isolated by a gap from the older, differentiated xylem further down the stem. The procambial strand itself, on the other hand, is usually continuous longitudinally.

The subsequent tracheids of the strand are added to the first in an upward direction towards the leaf primordium, and some are also added alongside the first tracheid, but comparatively few below it. The gap persists for some time, but is eventually closed by two downward branches of short tracheids, which border the gap and continue their downward course of differentiation in the internode below, alongside the xylem already there. The influence of a leaf rudiment on the course of differentiation in the stem extends at least beyond the first node below and may extend for four or five internodes in some cases. When the leaf traces later become merged in the general mass of secondary wood it is no longer possible to be certain of their identity, but there is some evidence that even in the lower part of the stem they act as physiological units and are influenced by the growth of the leaf they serve, so long as it persists.

The most important point is that the differentiation begins at the leaf base and extends from there first upwards then downwards.

The isolated uppermost tracheid, rich in soluble materials due to the breakdown of its protoplasm, acts as an osmotic cell, drawing water upwards from the xylem below and thus promoting growth around it. It forms the focus of a growth unit which extends from the leaf base downwards to the point, which may be several internodes below, at which the leaf trace is linked to the vascular system. Each such region grows independently, the lowest cells vacuolating first, the uppermost expanding last and continuing growth longest.

These first elements of the vascular system are generally known as the **protoxylem** and **protophloem** respectively, two names which have figured largely in descriptive anatomy. Their significance lies in their being the starting points for xylem and phloem differentiation respectively and thus determining the pattern of that development. The later-formed tissues are called **metaxylem** and **metaphloem,** and attempts have been made to distinguish the two stages on structural details (Fig. 844). Protoxylem elements are usually narrower than those of the metaxylem and their wall thickening is usually spiral or annular. They are also usually formed in parts which are still actively elongating, so that they are stretched passively after formation. Metaxylem elements are usually wider and shorter, are not stretched after their formation and are mostly pitted or scalariform. But none of these distinctions is absolute or complete, and it is not possible to separate clearly the two sorts of xylem tissue. This applies with even more force to the phloem, where there is no histological distinction between protophloem and metaphloem. We are only justified in keeping the two sets of terms to mark successive stages in ontogenetic development, and it has been well said that " the point about protoxylem is where it begins, not where it ends."

The earliest xylem elements are subject to a varying amount of stretching after they are fully differentiated. This may lead to the rupture of their end walls, so that open connection between tracheids is established and a "vessel" is formed. Protoxylem may therefore consist of either tracheids or vessels, but the difference in this case is accidental and irregular. Stretching of the protoxylem may break down the longitudinal walls as well as the transverse walls, so that the whole element collapses. Nothing then remains of the protoxylem but an intercellular cavity containing disorganized rings or spirals of lignin. This is often observable in mature stems.

Very different is the course of events in the formation of the mature type of vessel in the metaxylem. Here the individual cell elements may be either long or short, but in either case they expand transversely at a very early stage, even while still in contact with the cambium, until they are considerably broader, sometimes several times as broad, as the neighbouring tracheids. Their transverse walls are dissolved, wholly or in part, before thickening takes place, so that an open tube results, in which lies a file of separate protoplasts. A visible cytoplasmic pattern then develops, which determines the pattern of lignification, and this is continuous through many protoplasts, which shows that although separate they are subject to some common influence. Transverse expansion may continue during lignification, and the pits may then become extended like transverse slits in the completed woody wall. If these slits form a regular longitudinal succession the element is called scalariform, but such elements are uncommon in Angiosperms as compared with Pteridophytes.

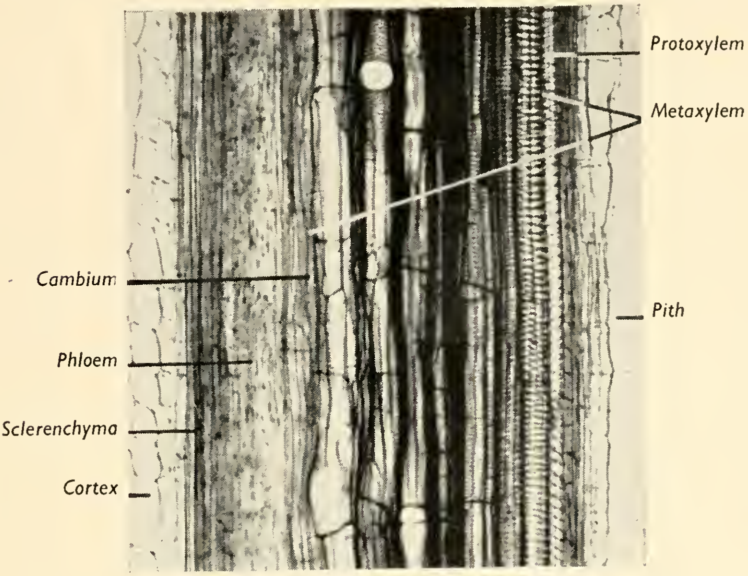

FIG. 844.—*Helianthus rigidus*. Longitudinal section through a primary vascular bundle of the stem showing various types of vessel thickening.

The effect of a common influence extending from cell to cell is also seen in the formation of Sanio's trabeculae. These are bars running horizontally across the lumen of tracheid cells. They are always radial and may run continuously across several cells, even across the cambium into the sieve tubes of the phloem. They originate as folds in the radial walls of the cambial cells, followed by a partial solution of wall substance which separates them from the wall, while in the xylem cells they become lignified. If they serve any specific purpose it is probably that of support against radial growth pressures. They are common in Conifers, but have also been found in a few Dicotyledons.

The transverse expansion of metaxylem elements is associated with the cessation of elongation in the internode, but this is not a sudden change, so that gradations between protoxylem and metaxylem naturally occur. Typical of the transitional zone are the reticulate elements, in which the spiral band, characteristic of protoxylem, gives place to a network of lignin, derived apparently from the close turns of an unstretched spiral, which have become connected at intervals, enclosing areas of unlignified wall.

The first protophloem elements appear in connection with the young leaves between the third and sixth from the apex. They are true sieve tubes, but small and without companion cells, and they are usually obliterated at about the level of the twelfth leaf. Like the protoxylem they are thus characteristic of the zone of elongation. They are replaced by the larger and longer-lived metaphloem sieve tubes, which have companion cells.

Sieve tubes form anastomosing strands of elongated, thin-walled cells, their essential distinction being that their contents are connected longitudinally through the perforations of the sieve plates. Protoplasmic connections between sieve tubes and companion cells or parenchyma cells may also exist, but they are of the common type and have not usually the structure of true sieve plates. The separation of the companion cell from the sieve tube mother cell is one of the last steps in phloem differentiation, and the separating wall may thus remain very thin and is sometimes without pits or plasmodesma.

The development of a sieve tube cell is marked by the disappearance of the nucleus and by a partial breakdown of the cytoplasm, which becomes completely permeable, coarse and ill-defined. Although still living in the mature element and capable of cyclosis, it is moribund and does not survive for long. The products of disintegration accumulate as slime in the central vacuole and give rise to the " slime plugs," which may be seen in fixed material.

The ontogeny of the sieve plates cannot be described with certainty, but the mature plates have some recognizable features in common. There is a basic framework of cellulose, in which are large perforations, so that it forms a network. The meshes are lined with " collars " of a polysaccharide of uncertain composition called **callose** (or callus). Through the tubes thus formed the protoplasm of the adjacent elements is continuous. The amount of callose tends to increase, at first lengthening the connecting pores through the plate, and then narrowing and at last closing them. A massive cushion of callose may then develop on both sides of the plate, which normally ends the active life of the sieve tube, though there is evidence that in some plants, like *Vitis*, the callose pad may form temporarily during the first winter and then be dissolved in the spring, only to reform permanently in the second winter.

Where sieve tubes are in lateral contact there are often connections between them, formed on the longitudinal walls. They are called **sieve fields** and seem to be closely similar to sieve plates in structure, though smaller and less clear.

The walls of the sieve tubes are of cellulose, but in a highly hydrated state. When mature the wall is thick and soft and has a distinctive pearly lustre, like collenchyma.

Summary of Elementary Structure

Stems always bear **leaves,** either green **foliage leaves,** modified **floral leaves** or reduced **scale leaves.** These are attached to the stem at joints or **nodes** and are separated by lengths of bare stem called **internodes.** The leaves develop at the apex of the stem, arising as little cushions of cells on the sides of the dome-shaped **apical meristem** (Fig. 845).

In the apical meristem vascular tissues develop as strands which enter the base of each developing leaf. These are called **vascular bundles,** and they are also **leaf traces,** for every bundle supplies a leaf. Some distance below the leaf base, usually at least two internodes below and sometimes more, the leaf trace bundles are attached to older bundles, so that they form part of a continuous system.

Vascular bundles consist of **xylem** on their inner sides and **phloem** on their outer sides (Figs. 846 and 847). Between the two lies a narrow belt of **cambium,** whose cells are tangentially flattened and arranged in radial rows. These cells repeatedly divide tangentially, producing cells which develop into xylem cells or phloem cells according to the side of the cambium on which they lie. The vascular tissues of the bundles thus continue to expand radially throughout life.

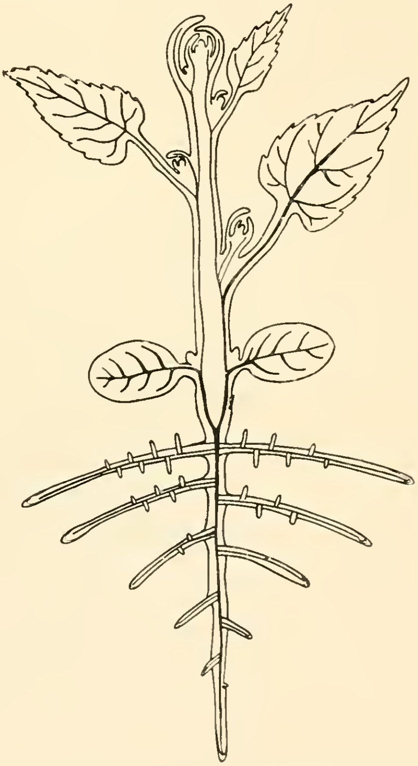

Fig. 845.—Diagram of a theoretical plant form showing the relationships of the various principal structures. The vascular system is indicated by black lines. (*After Sachs.*)

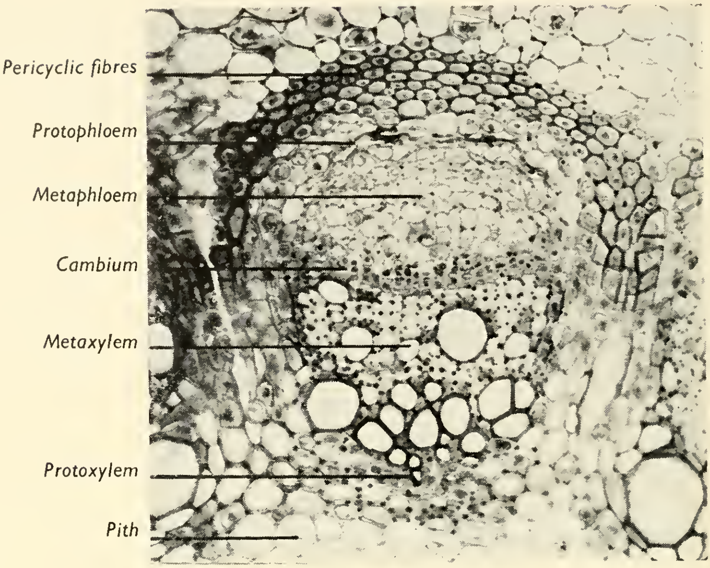

FIG. 846.—*Menispermum canadense.* Dicotyledon. Transverse section of a primary vascular bundle of the stem.

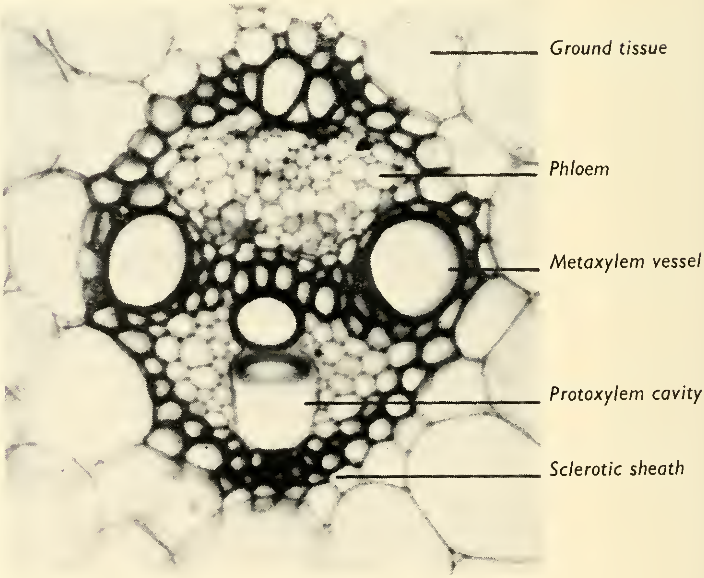

FIG. 847.—*Zea mais.* Monocotyledon. Transverse section of a vascular bundle of the stem.

Xylem consists of **tracheids,** which are individual cells, and of **vessels,** which are files of cells opening into one another longitudinally to form long, open tubes. The walls of these cells are lignified in various patterns, usually spiral or annular in the earliest part formed, known as **protoxylem,** which lies next to the pith; and reticulate or pitted in the later-formed tissue, called the **metaxylem.** There are also present **xylem parenchyma** cells with lignified walls and **fibre cells.** Of all these xylem cells only the parenchyma have any living contents.

Phloem consists of **sieve tubes,** which are united longitudinally through perforated end walls called **sieve plates,** through which the cytoplasm is continuous. Sieve tubes have degenerate cytoplasm, but no nuclei, and are short-lived. Their walls are formed of thick, soft cellulose. They are accompanied by long, narrow **companion cells,** and often by **phloem parenchyma** cells.

In Dicotyledons the number of trace bundles to each leaf is usually small and they form a single ring in the internodes, separating the **pith** inside from the **cortex** outside (Fig. 848). The cambium is continued across between the bundles as the **interfascicular cambium,** from which develop secondary tissues on both sides. If these consist only of parenchyma cells the bundles of the ring remain separated by broad parenchymatous **primary medullary rays** (Fig. 849). If the interfascicular cambium forms xylem and phloem tissues, these serve to unite the vascular bundles into continuous rings, which are added to annually so long as the plant lives, and in time may build up the masses of wood which are characteristic of timber trees. Each yearly increment is distinguishable in the wood as an **annual ring** (Fig. 850). Similar annual rings are added to the phloem, but are much narrower and seldom visibly distinct. Narrow **secondary medullary rays** are also formed in the secondary vascular tissues and persist through their whole thickness (Fig. 851). In small herbaceous plants there may be no cambium.

In Monocotyledons the leaves usually have broad bases and many leaf-trace bundles. The stem is crowded with bundles, which do not lie in a regular ring (Fig. 852). As a rule the leaves are set close together, and internodes may be very short or non-existent. Only in a few rare cases is there any cambium or any secondary growth in a Monocotyledon.

Outside the ring of bundles in a Dicotyledon there may or may not be a visible **endodermis,** but there is usually a **pericycle,** consisting chiefly of woody fibres. In Monocotyledons both these may be absent.

Outside these layers lies the parenchymatous cortex, bounded externally by the **epidermis.** When secondary growth has commenced a new cambium, called the **phellogen** or **cork cambium,** appears, variably located somewhere between the limits of the phloem and the epidermis in different species (Fig. 853). Its cells produce **phellem** or **cork** outwardly, and often also **phelloderm** or **secondary cortex** inwardly. The cork cells are suberized and impervious to water. They are, therefore, dead cells and form an impervious coating to the stem, which replaces the earlier epidermis. The whole phellogen system is collectively termed the **periderm.**

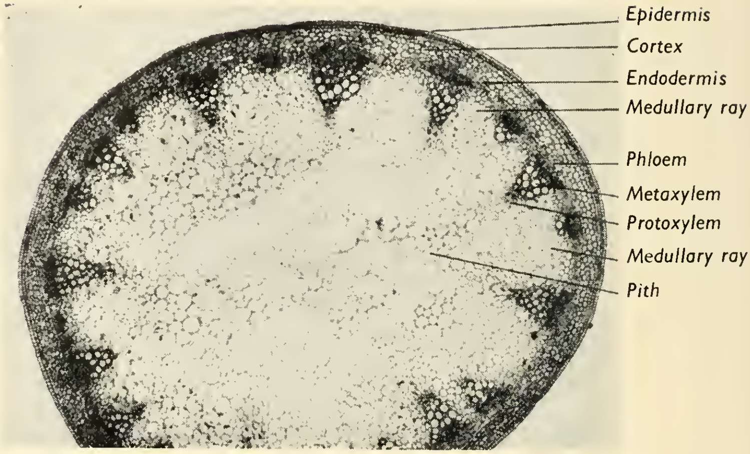

FIG. 848.—*Tropaeolum majus.* Dicotyledon. Transverse section of the stem showing a single ring of primary vascular bundles separating the pith from the cortex.

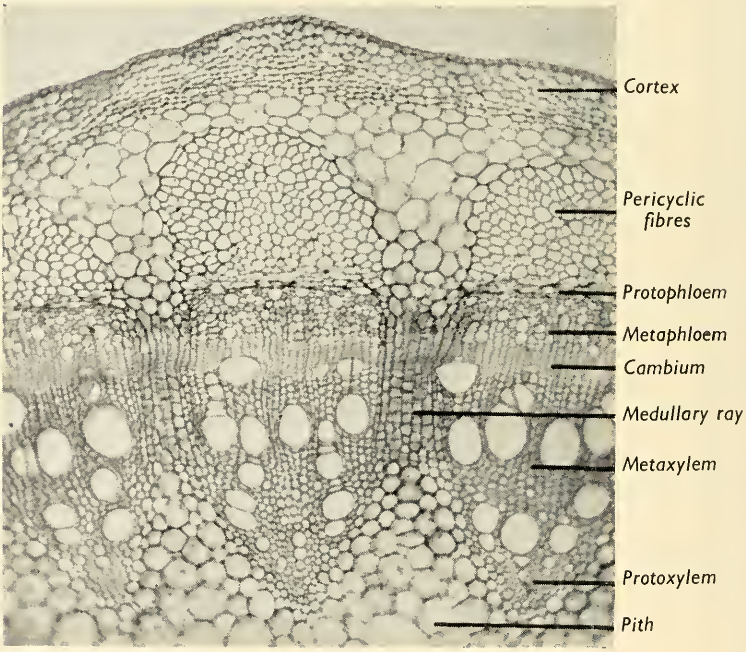

FIG. 849.—*Helianthus rigidus.* Transverse section of a part of a stem in an early stage of secondary thickening showing the primary medullary rays crossed by the interfascicular cambium.

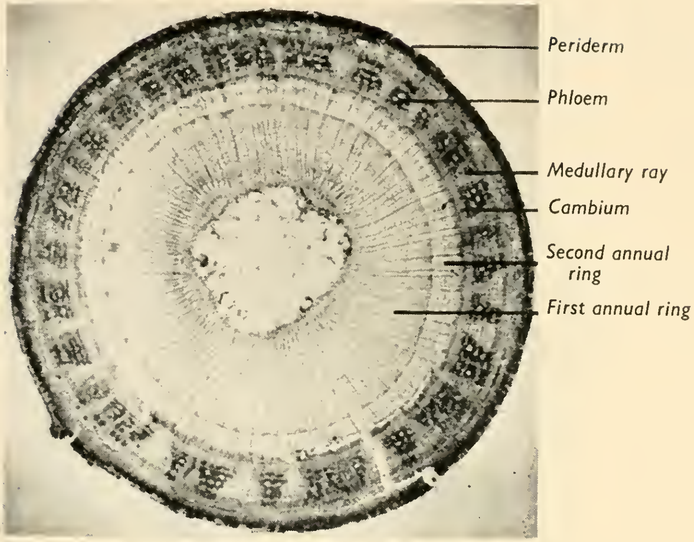

FIG. 850.—*Tilia vulgaris.* Transverse section of a secondarily thickened stem showing two annual rings and early periderm formation.

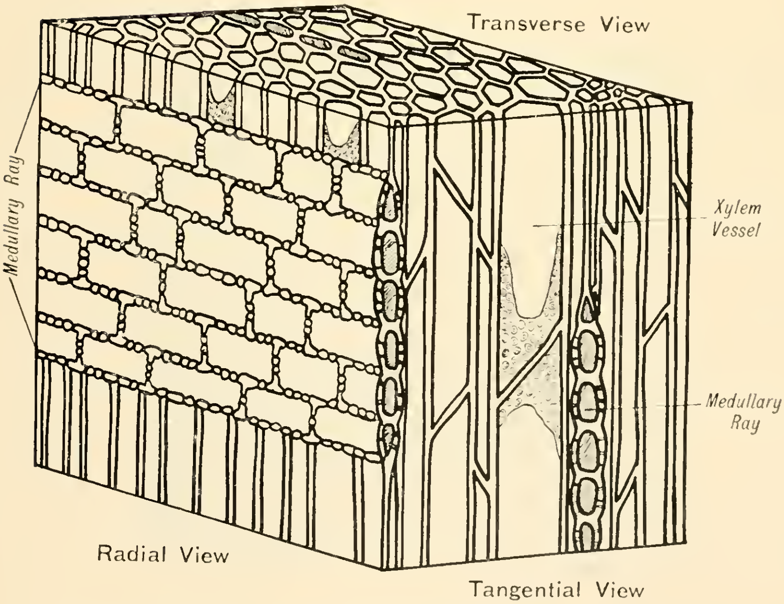

FIG. 851.—Diagram showing a three-dimensional view of the secondary xylem in an Angiosperm, illustrating the relation of the medullary rays to the conducting elements.

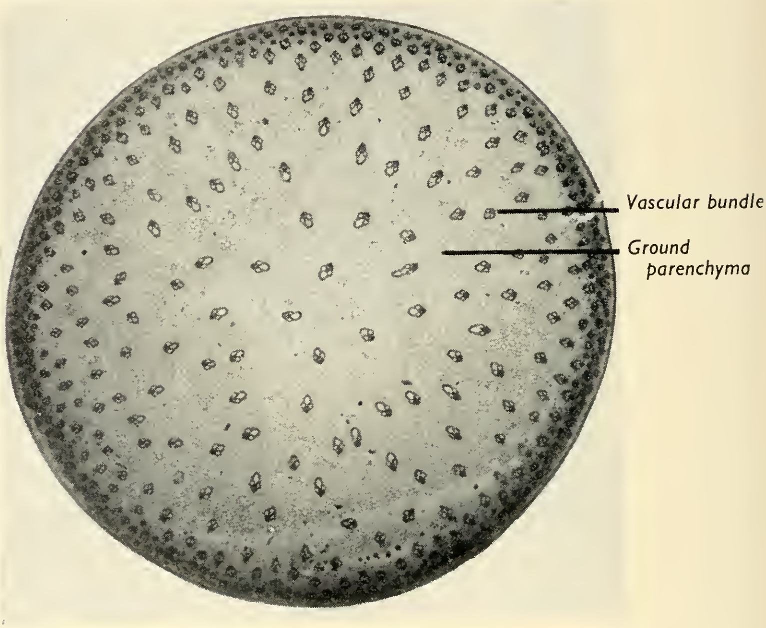

FIG. 852.—*Zea mais.* Monocotyledon. Transverse section of the stem showing scattered vascular bundles.

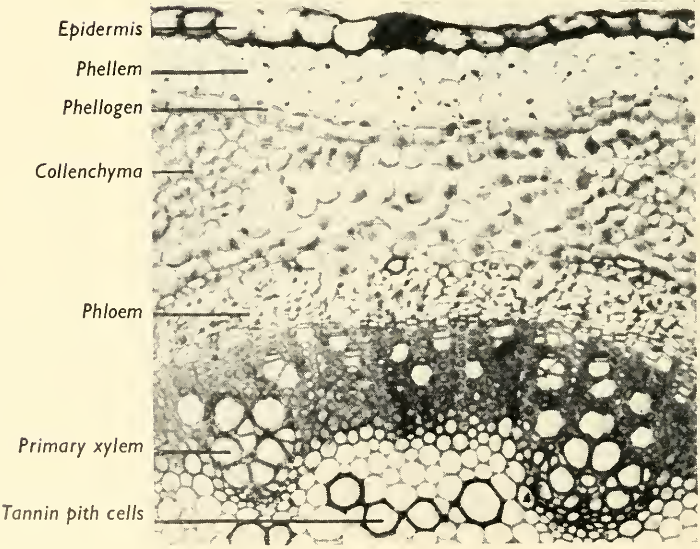

FIG. 853.—*Sambucus nigra.* Transverse section of the stem in an early stage of secondary thickening showing the phellogen and phellem.

The continuity of the cork layer is interrupted at numerous points by clusters of rounded cells, corky in nature but so loosely packed that air can readily penetrate between them. These are the **lenticels,** which allow access of air to the living tissues within (Fig. 854) (see also p. 878).

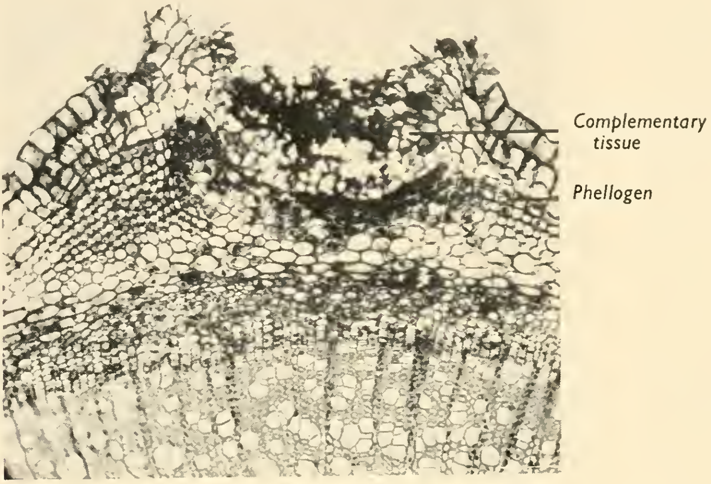

FIG. 854.—*Sambucus nigra.* Transverse section of a woody stem with lenticel.

ANATOMY OF THE MATURE STEM

1. *The Epidermis.* The essential character of an epidermis is that it is a protective layer, or, in other words, that it is a barrier between the internal organization of the plant and the environment. This protection is not exclusively concerned with water loss, though that is a very important factor, and the surface layer of some submerged aquatics may be truly classed as an epidermis even though it is not a protection against desiccation. But the emphasis on the barrier function excludes from this category secretory surfaces such as those of glands, and absorptive surfaces such as those of the young root. Furthermore, a true epidermis is a primary layer, developed from the apical meristem, and the name does not apply to the exodermis of roots or the periderm of older stems, which are both secondary.

On the other hand, certain specialized cells of the surface layer, such as hair cells and sclereids, which may not be primarily protective in function, are none the less morphologically part of the epidermis and we shall treat them as such.

Epidermal cells are usually described as tabular in form, which means somewhat flattened radially, but when viewed from the outer surface they are seen to be nearly always vertically elongated, and they are by no means always radially flattened. In outline they vary greatly, but the variation is much less in the epidermis of the stem than in the leaf. Growth of the primary stem is chiefly elongation, and the epidermal cells in the young state are consequently elongate and narrow. The radial walls may be somewhat wavy, which is apparently the result of continued expansion of the cells after growth of the stem has ceased. The same factor may result in the outer surfaces being convex, domed or even papillate. The radial walls are not only undulating, when viewed from the exterior, but are thin and have numerous large pits. This implies that lateral movement of water in all directions in the epidermis must be relatively easy, and it is probable that a dangerous loss of water at any one point of the surface may be compensated by the tangential flow of water towards the threatened spot from other parts of the epidermis, which thus acts as a first line of defence, before the radial flow from the xylem can become effective. That epidermal cells do, in fact, part with considerable amounts of water at times, is shown by the great changes of volume they can withstand without injury, especially in leaves. When this occurs the radial walls shrink and the cells become flattened, but they rapidly expand when equilibrium is restored.

The epidermal cells of some plants (*e.g.*, *Erica* and *Daphne*) have greatly thickened, mucilaginous inner walls, thus providing for increased water storage. The physiological as well as the mechanical cohesion of the epidermal cells is increased by the absence of any spaces at the angles between them.

The outer surface of the epidermis is covered by the **cuticle.** This layer, which varies in thickness in general relationship to the moisture conditions in the environment, is extra-cellular and continuous and therefore helps to bind the epidermal cells together. It is tough and elastic, only slightly permeable to either water or gases, and its protective value is very great. Its development begins very early, and it may sometimes be traced even on the tunica in the meristem.

Priestley has explained it as a non-volatile residue from the surface evaporation of sap, and while this would serve to account for its greater thickness in plants of dry habitats, it is difficult to accept so simple an explanation for cuticles on enclosed surfaces, such as the inner wall of the ovary or on leaves within the winter bud. The cuticle contains no cellulose and is composed chiefly of the insoluble anhydrides of an unknown number of fatty acids, of which two, stearocutic and oleocutic acids, have been described. They probably reach the epidermis in the form of glycerides, *i.e.*, as true fats, and are there decomposed, with the liberation of the free acids.

The chief difference between cuticle and suberin, apart from their different location in the plant, seems to be the absence from the former of the phellonic acid which is an important constituent of the latter. Their reactions to microchemical test reagents are very similar.

Continued growth of the epidermis, besides causing the wavy outlines of the cells, also throws the cuticle covering into wrinkles, which often form a minute pattern over the outer surface of each cell.

The cuticle often extends downwards for some distance along the radial walls, forming distinct wedges between the cells, but it never completely separates them. Below the cuticle proper lies the **cutinized layer,** which is formed by the cellulose outer walls of the cells, more or less impregnated with cutin. It is sharply separated from the true cellulose wall next to the cell lumen. The cutinized layer is not invariably present, but when it occurs it is frequently much thicker than the true cuticle and may be the chief protective layer. It often accompanies the cuticle in forming prominent wedges between the radial walls of the cells (see Fig. 445).

Beneath the epidermis there is often, in plants of dry or exposed habitats, a second, or even a third, specialized layer, the walls of which are not cutinized but may be greatly thickened with cellulose or lignin, or else may be quite unthickened. It may augment both the protective and the water storage functions of the epidermis, and it is referred to either separately as the **hypodermis,** or both layers together may be termed a **multiple epidermis.** Strictly speaking, the latter name should not be used unless it is known that both layers of cells have originated from the dermatogen by tangential cell divisions. As this cannot often be proved it is best to retain the general term hypodermis.

The epidermis of young, green stems contains a number of **stomata,** which resemble those on the leaves. Their structure will be fully described in Chapter XXII. They are not normally so numerous as on the leaves, but in plants with reduced or abortive leaves they may be the only means for gas exchanges with the atmosphere, and in such cases they have the same importance in photosynthesis as those on normal leaves.

2. *Epidermal Outgrowths.* Outgrowths of the epidermis take many forms and are included under the general term **trichomes,** which covers not only true hairs, but other modified structures such as glands and prickles. Their typical forms have already been described in Chapter XIII. They are, of course, not confined to the stem, but no distinction can be drawn between organs in this respect, since identical trichomes may be produced at all points on the surface of the shoot. Their distribution is, however, often restricted to definite lines or areas and may be a mark of distinction between related species.

Despite the immense variety among trichomes, a complete anatomical series may be traced between the simplest, which are merely prolongations of a single epidermal cell, and massive structures which arise from groups of cells and involve also the sub-epidermal tissues and may even receive one or more vascular bundles. These extreme cases have sometimes been distinguished as **emergences,** but in spite of their apparent differences no sharp line can be drawn between them and the simpler trichomes.

Hairs can be classified under three main types: simple, branched, and peltate. Simple and branched hairs may consist of one or of many cells. The branched types are sometimes quite elaborate, like small bushes; or they may be flattened, the branches forming a rosette around a short stalk-cell. The latter type is related to the peltate or scale hairs, which are similar to flattened branched hairs but with the branches cohering into a disc. These discs, if they overlap, as in the Eleagnaceae, form a complete protective armour over the surface of the epidermis.

Secretory hair glands may be simply swollen cells which are usually water stores ; or they may be compound, with long or short stalks bearing a head consisting of either one large secretory cell, or a more or less peltate group of cells. Some of these types are illustrated in Volume IV in connection with insectivorous plants.

Prickles are classified as trichomes, no matter how massive they may be, whenever it is clear that they arise from the epidermis and are not modifications of any other organ. As a matter of fact the large prickles of *Rosa* and the vascular prickles on the fruit of Horse Chestnut are connected with simple hairs by all gradations of finer prickles. Prickles of all grades may even be present together on the same stem, as in the Burnet Rose (*Rosa spinossissima*), and it is notable that in some Roses the prickles at the nodes are often much larger and stronger than the others. The so-called " endogenous prickles " on the stems of some Palms are, however, really modified adventitious roots and are therefore properly classified as thorns. The very large and prominent spines of the Cacti are of doubtful nature, having been interpreted both as modified leaves and as trichomes. They grow from little humps, called areolae, from which the lateral buds, if any, usually arise, and the balance of evidence points to the spines being really trichomes.

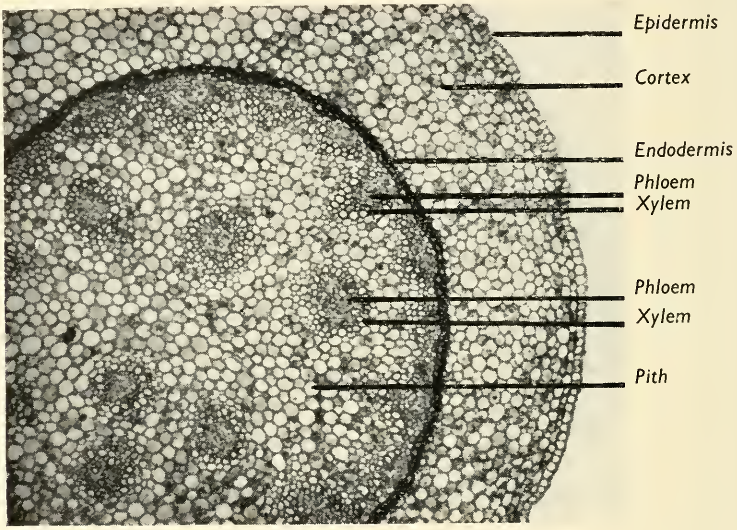

Fig. 855.—*Convallaria majalis.* Transverse section of rhizome showing the broad cortex and well-marked stele with endodermis.

3. *The Cortex.* Between the epidermis and the stele lies the zone of the parenchymatous **cortex.** In stems it is rarely as broad as in the root, for the vascular tissues, probably for mechanical reasons (see p. 912) lie much nearer to the periphery than in roots. The underground stems of Monocotyledons usually have a fairly broad cortex (Fig. 855), but monocotyledonous aerial stems, such as that of the Maize (Fig. 856), so often used as an anatomical

type, are as a rule only temporary flowering shoots and may have a very narrow cortex or none at all. Such stems may be regarded as being either entirely stelar or else as having no stele. There is at any rate, in many cases, no stelar boundary visible. Where a cortex is present it often contains numerous and small marginal leaf traces.

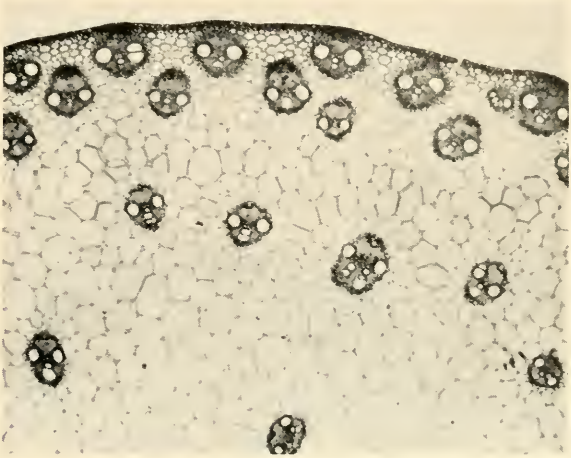

FIG. 856.—*Zea mais.* Transverse section of stem showing absence of cortex and vascular bundles in contact with hypodermis.

FIG. 857.—*Anthriscus sylvestris* (Umbelliferae). Collenchyma in the cortex of the stem.

The outer zones of the cortex frequently form a **collenchyma** either in a continuous band or, in angular stems such as those of Labiatae and Umbelliferae, developed only below the ridges (Fig. 857). Collenchyma is definitely a mechanical, strengthening tissue. It has this great advantage over sclerenchyma, that its cells are living and growing and hence it is able to adapt itself to the growth of young organs. It is chiefly characteristic of such organs, nevertheless in short-lived structures such as petioles or the herbaceous stems of Dicotyledons it may remain as the permanent mechanical tissue. The aerial stems of Monocotyledons, on the other hand, depend for mechanical support more on the development of the sclerotic sheaths around their vascular bundles than on collenchyma.

As collenchyma cells remain alive it follows that their cell walls cannot be uniformly thickened, for this would cut them off from all external supplies. The thickening material, which is of cellulose, is accordingly distributed in such a way that thin walls are left at certain parts of the cell to allow of intercommunication. Frequently the thickening appears only at the angles of the cells, while in other cases it may be all on one side or on two sides, an arrangement which also has the advantage of increasing the plastic and yielding character of the tissue as a whole. The cells are somewhat elongated vertically, but never to the extent of woody fibres, and they may be regarded as mainly parenchymatous.

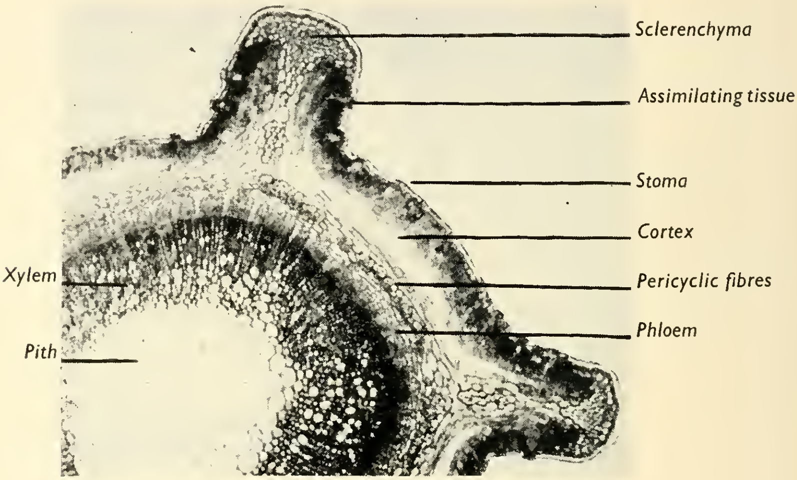

Fig. 858.—*Sarothamnus scoparius.* Transverse section of stem showing ridges with sclerenchyma, and assimilating tissue in the cortex.

Cortical cells usually contain functional chloroplasts since light can penetrate a distance up to 100 μ from the surface. True palisade tissue, comparable with that in the leaf, may be found in the cortex of some xerophytes, either in succulents of the Cactus type or in switch plants, like the Broom (Fig. 858), in fact, wherever the stem has taken over the function of photosynthesis from the leaves, either owing to the reduction of the latter to mere scales or to their complete disappearance.

Where **chlorenchyma,** *i.e.*, chloroplast-containing tissue, is present, whether of the palisade form or not, there will usually be some water storage tissue closely adjacent to it in the cortex. The cells of such a tissue are large and thin-walled, and they not infrequently contain mucilage. As it is nearly always in xerophytes that chlorenchyma occurs in the cortex the advantage of a water reservoir close at hand is obvious. Indeed, in the Cacti, where the stele is often relatively slender, the greater part of the stem tissue is water-storing cortex, only a narrow outer zone being chlorenchymatous. Internal glands and sclereid cells are frequently present in the cortex, the latter being sometimes complexly branched and forming an important part of the skeletal system of the plants (*e.g.*, Magnoliaceae) in which they occur. More often, however, they are isolated and scattered and not of significant mechanical value.

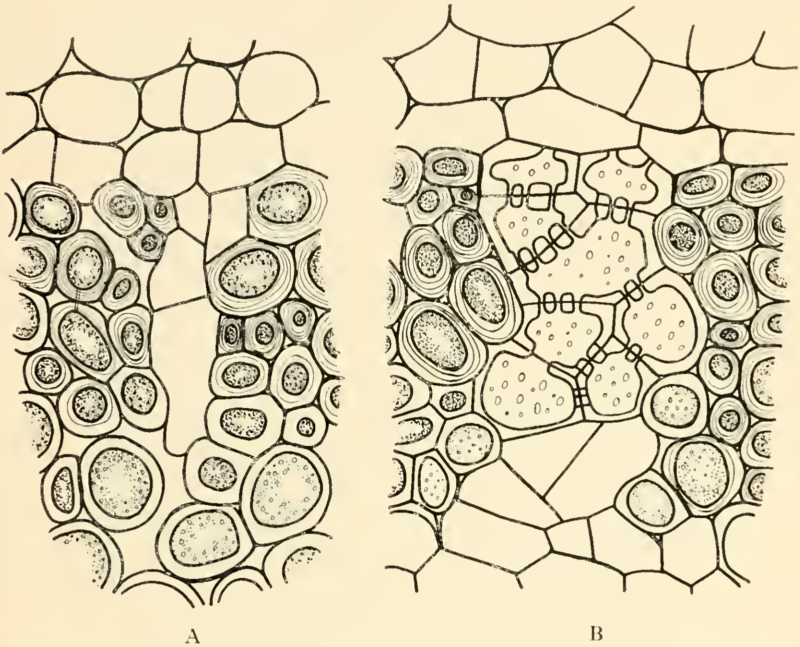

FIG. 859.—*Aristolochia sipho.* Breakage of the zone of pericyclic fibres due to radial growth of the stem and its repair by the ingrowth of parenchyma cells from the cortex, which become lignified sclereids. (*After Haberlandt.*)

After elongation of the young stem is over, a ring of sclerenchymatous fibres may form in the cortex, as, for example, in Oak, Birch or Ash, supplementing the collenchyma as a strengthening tissue. Growth in girth soon and repeatedly ruptures this ring, but the gaps are made good by the ingrowth of parenchyma cells into the radial spaces due to the ruptures, and their transformation into sclereids (Fig. 859). Thus a composite mechanical ring is formed of arcs of fibre cells separated by arcs of sclereids.

One of the most striking departures from normal cortex formation is to be seen in aquatics, where the cortex (Fig. 860), or in the case of Monocotyledons the whole ground tissue (Fig. 861), is divided into large air spaces, separated by membranes only one cell thick. These lacunae are limited in length to one internode in Dicotyledonous stems, and even in Monocotyledons they are not of great vertical length, but the horizontal membranes which separate them are perforated by minute intercellular passages, which form at all the angles of the cells. These provide for the movement of air

FIG. 860.—*Myriophyllum spicatum.* Transverse section of stem showing central stele and large radial air spaces in the inner cortex.

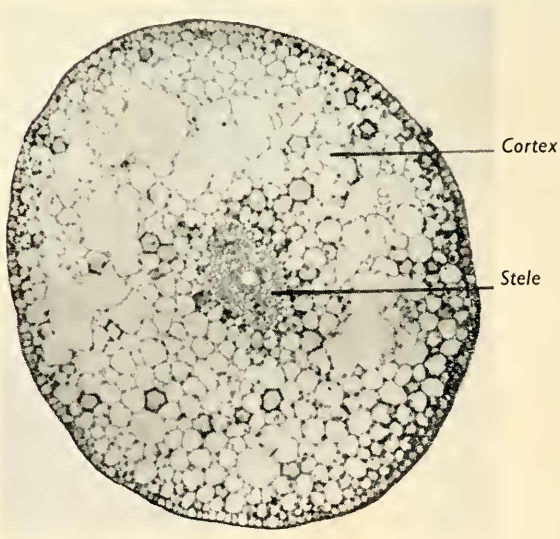

FIG. 861.—*Potamogeton sp.* Transverse section of stem showing reduced stele with one central vessel and irregular air spaces in the ground tissue.

from one lacuna to another, but they are too small to allow water to penetrate, if it should chance to get into one lacuna through an injury to the epidermis. They are in effect waterproof bulkheads and prevent the accidental flooding of the whole internal air system (Fig. 862).

4. *The Periderm.* The epidermis is usually only retained for a short time while the shoot is young, and it is later replaced by a secondary covering. This is necessary because the thick walls and the cuticular layer of the epidermis inhibit the division of its cells. The epidermis can therefore only accommodate itself to the increasing girth of growing stems by the tangential stretching of its cells, and that is limited in extent.

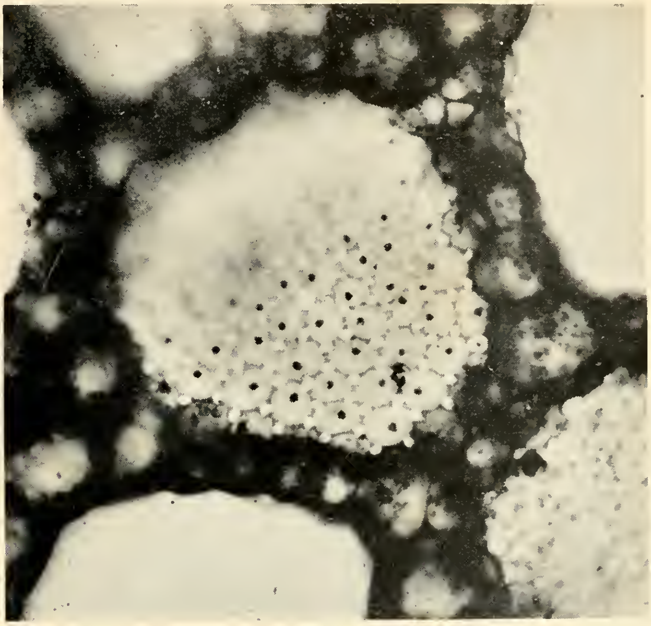

FIG. 862.—*Potamogeton natans.* Transverse section of stem showing one of the transverse membranes with small intercellular passages.

A few cases exist of woody plants which retain their epidermis for a number of years, *e.g.*, *Laurus*, *Aucuba*, *Rosa*, *Acer*. The cuticle is soon ruptured by the growth of the stem, but the cutinized cell wall increases enormously in thickness and is progressively regenerated from within, while the outer layers crack and crumble away. Most smooth-stemmed shrubs do, however, eventually form a bark. One exception is the Mistletoe, in which the primary epidermis is supplemented by further cutinized layers of cells formed successively inwards, so that a multiple epidermis of great thickness is built up.

Only a growing tissue can retain permanently its equilibrium with other growing tissues, and thus the secondary covering of the stem is initiated by the formation of a cambial layer known as the **cork cambium** or **phellogen,** the chief product of which is the **phellem** or cork. The phellogen is a true secondary cambium formed by the rejuvenation of tissues already fully differentiated, which may be situated anywhere between the secondary phloem and the epidermis itself, although in most cases the first phellogen lies in the cortex near to the outer surface (Fig. 863). It is a single-layered meristem, and by tangential divisions it cuts off a succession of cells outwards, which are arranged in radial rows, corresponding to the cells of the phellogen from which they have arisen. There are a few examples of intraxylary phellogens, *e.g.*, *Artemisia*, where cork formation begins in the wood of the current year, forming a sleeve over the wood and ending upwards in a dome in the pith near the stem apex, thus isolating all new growth from the old. This may be related to the desert conditions under which the plants concerned chiefly live.

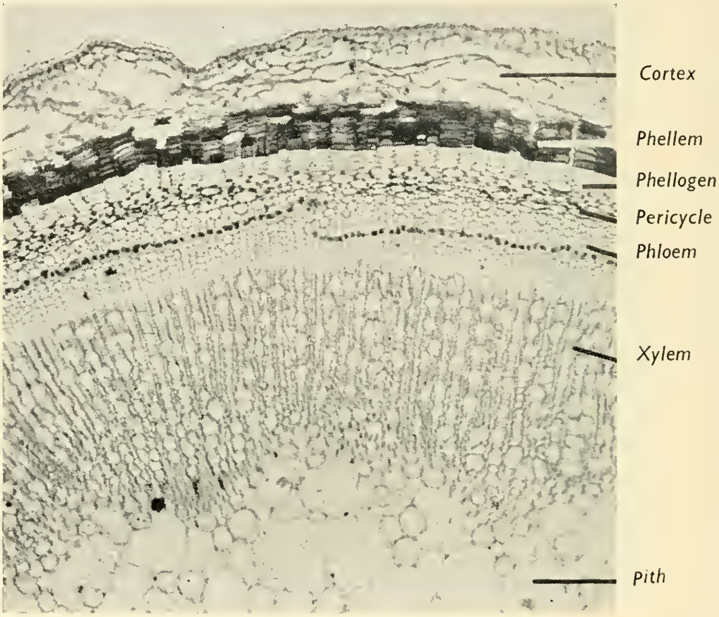

FIG. 863.—*Ribes rubrum.* Transverse section of a woody stem in its second year showing phellogen formed in contact with the pericycle.

Priestley has shown an association between phellogen formation and the existence of some anatomical barrier to outward sap diffusion. When a functional endodermis is present this acts as such a barrier and the phellogen commences in the pericycle. In the absence of such an endodermis there may be no corresponding barrier until the hypodermis or the epidermis is reached, and it is there that phellogen appears. Intermediate cases may be accounted for by the presence of an internal cuticle at some level in the cortex or by the existence of an impermeable sclerotic layer. According to Priestley's view the accumulation of sap on the inner side of a diffusion barrier provides the physiological stimulus to increased cell division. As the cell sap always contains diffusible fatty substances the materials for the formation of suberin in the cork layers are also accumulated at the level of the phellogen.

The suberization of the walls of phellem cells consists in the deposit of a layer of suberin, unmixed with cellulose, between the middle lamella and the inner wall of pure cellulose. This layer varies greatly in thickness in different cases, and in the massive " cork wings " (Fig. 864) on the branches of species of some trees, such as *Ulmus* and *Acer*, it may be practically absent, which has led to the application of the term **phelloid** to such unsuberized cork tissues. The suberin itself is apparently a mixture of the anhydrides of fatty acids, the chief of which is phellonic acid, $C_{22}H_{43}O_3$, and it is thus closely similar to cutin. Both substances seem to be dependent on contact with air for their development.

Fig. 864.—*Ulmus glabra* var. *hollandica*. Transverse section of a small branch showing cork wings.

There are no pits through the suberin layer, and as it is highly impermeable the suberized cell soon dies. Tannin and related substances often accumulate in the cells before suberization, and these give the cork its dark colour and its value for tanning leather.

Haberlandt showed that the protective value of two-year-old cork layers against evaporation is about the same as that of the primary epidermis. That it is not greater is probably due to the cracking, caused by growth pressure, which fissures the outer layers of the cork, and would destroy its protective value if fresh layers were not constantly added from within by the phellogen. The heavy cork layers of old stems are highly protective.

The formation of a cortical or other superficial phellogen begins below the stomata, and is preceded by cutinization of the cells lying beneath the stomatal openings. The phellogen formed at these spots is highly active and cork formation is in progress there before the phellogen has spread round the stem as a continuous layer. The excess of cork cells formed, ruptures the epidermis around the stoma, and protrudes above the general surface level as a spongy mass called the **complementary tissue.** Such a spot is clearly visible to the eye on the stem surface and is called a **lenticel.** Blockage of diffusion through the lenticels, due to the formation of a closing layer of compact phellem in the autumn, reacts upon the phellogen and stimulates increased divisions, thus bursting through the block in the spring. The life of a lenticel seems to be an alternation of blocking and bursting phases. Permanent lenticels are not in all cases formed at every stoma, the number being related to the vigour of the shoot. In deep-seated phellogens, both primary and secondary, the lenticels are obviously not related to stomata and their distribution appears to be related rather to the broad medullary rays which are associated with the leaf traces.

Lenticels have been interpreted as ventilating apertures, but their causation has nothing to do with the assumed necessity for this function. Suberin is, however, exceedingly impermeable to air, and the rounded and irregularly arranged cells at the lenticel undoubtedly do allow access to the underlying tissues for air, which cannot penetrate at any other point. The physiological value of this is reflected in the bad effects on the health of the plant which result if the lenticels become covered with external growths of moss or lichen.

While the chief activity of the phellogen is in forming phellem outwards, there is usually also a slow production of cells inwardly, which are added to the cortex and are known as **phelloderm** or secondary cortex. These cells are not suberized and are only distinguishable from the cortical parenchyma by their arrangement in radial files and sometimes by the presence of starch grains. Their walls are often thicker than those of the cells of the primary cortex and may even be lignified, as in *Canella*.

We thus see the elaboration of a secondary protective system consisting of phellem, phellogen and phelloderm which goes by the collective name of **periderm.** This slowly develops into the **bark** of old stems, but in this development other tissues become involved.

In smooth-barked trees the first phellogen remains active for some years and is only slowly replaced, if at all. The bark of such trees therefore consists of a continuous cork film (Fig. 865). In rough-barked trees, however, the first phellogen is soon replaced by a series of others, lying successively deeper in the tissues, and all later phellogens, after the first few, are formed in the secondary phloem, much of which is destroyed in this way and its remains incorporated in the bark, along with dead cortex, collenchyma, sclerenchyma, etc. Bark is thus a composite structure. Where the later phellogens form continuous zones the bark may show successive annual rings, like the annual rings of the wood, each marking the formation of a new phellogen, but in many other cases the later phellogens form a series of discontinuous arcs and the bark is thus cut up into distinct areas, between which deep cracks appear. The various bark patterns on old tree trunks, which are characteristic of different species, are thus traceable to variation in the arrangement of the phellogen layers.

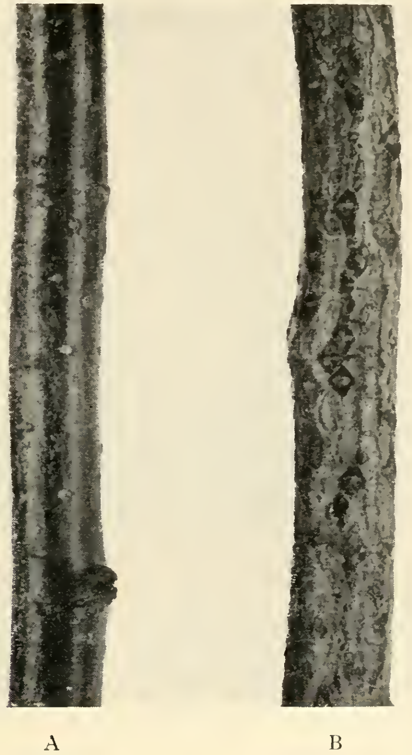

FIG. 865.—Types of bark. A, *Castanea sativa* (Sweet Chestnut). B, *Fagus sylvatica* (Beech).

An abnormal formation of cork is commonly associated with injuries, when it is known as **wound cork** (Fig. 866). Wounding or almost any sort of lesion of the integrity of the plant body may call it forth, and any living tissue may produce it. The first reaction to the wound is the suberization of the outer surfaces of exposed but intact cells. Suberization then spreads inwards for several cell layers. Below this barrier cell division starts and a cambium is organized which produces a few layers of regular cork cells, forming an impermeable barrier against desiccation, parasites and other inimical influences.

5. *The Endodermis.* The innermost layer of the cortex, surrounding the stele, is called, as in roots, the **endodermis** (see Chapter XIII). A typical endodermis, with Casparian bands, recognizably the same as that in roots, is not common in stems. The chief exceptions are among water plants, such as *Potamogeton* and *Hippuris*, in which the vascular tissues are concentrated into a relatively slender axial strand, as is normal in roots. Many other exceptions occur which are not, however, related to special environmental

FIG. 866.—*Ribes aureum.* Transverse section of an injured stem showing above, a layer of wound cork and below, a parenchymatous callus with fragments of pericyclic sclerenchyma. (*After Kuster.*)

features, *e.g.*, in some Compositae, species of *Primula*, and in the rhizomes of some Monocotyledons (Fig. 867). The endodermis, in most cases where it occurs in the stem, is a common investment round the stele as a whole, but there are a number of instances among Angiosperms where each vascular bundle has an individual endodermis (Fig. 868), which is not infrequently continued into the leaves (*Adoxa*, *Menyanthes*, and many Grasses, such as *Festuca*). Species even within the same genus may differ in this character as, for example, in *Ranunculus*, where *R. lingua* and *R. flammula* are peculiar in having individualized bundle sheaths.

The significance of the endodermis and of its variations cannot as yet be fully interpreted on physiological grounds, but some interesting points have been elucidated. It first appears outside the procambial zone at the stem apex,* simultaneously with the first appearance of xylem elements. Materials from the breakdown of the xylem protoplasm probably diffuse out radially, and may supply the fatty acids which condense to form the Casparian Band. It has been suggested that the condensation of fatty acids at this level is due to the penetration of air to this zone through the intercellular spaces of the cortex, but while we may have here the foundation for an explanation it is plainly not the whole story.

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* In Juncaceae and Cyperaceae it arises in the procambium. Its status as part of the cortex is not therefore universal.

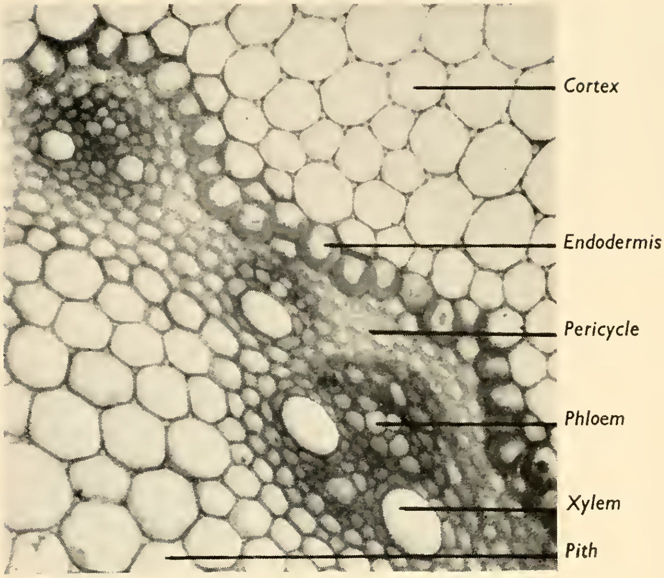


Fig. 867.—*Agropyron repens.* Transverse section of rhizome showing the strongly thickened endodermis.

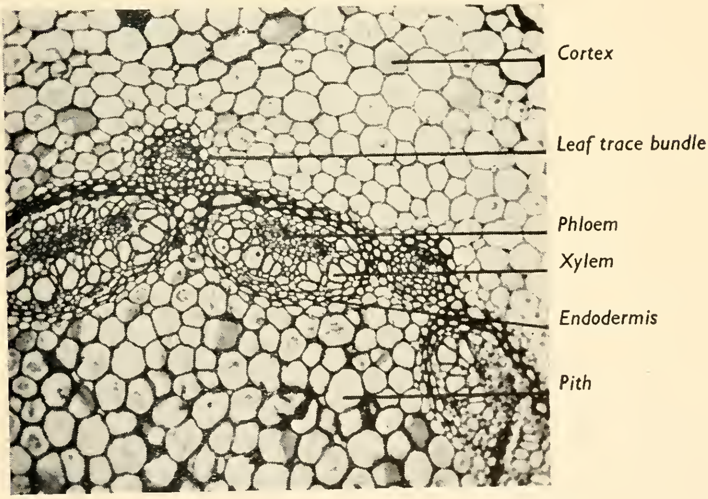


Fig. 868.—*Clintonia sp.* Transverse section of stem showing a ring of concentric vascular bundles each with its own endodermis.

The stele is not the only organ of the stem to possess a sheath, since many glandular passages are similarly protected, nor does the stelar sheath always have a true endodermal character. In a great many stems the layer surrounding the stele is marked by the presence of large starch grains, although the cells may not be otherwise different from those of the rest of the cortex, which may contain plastids but no large starch grains. This " starch sheath " corresponds morphologically to an endodermis, though it will avoid confusion if we do not apply this term to it, since it lacks the Casparian thickening and is physiologically different. Its morphological identity with an endodermis is shown by the fact that a starch sheath in a young stem may sometimes lose its starch and become thickened as an endodermis at a later stage.

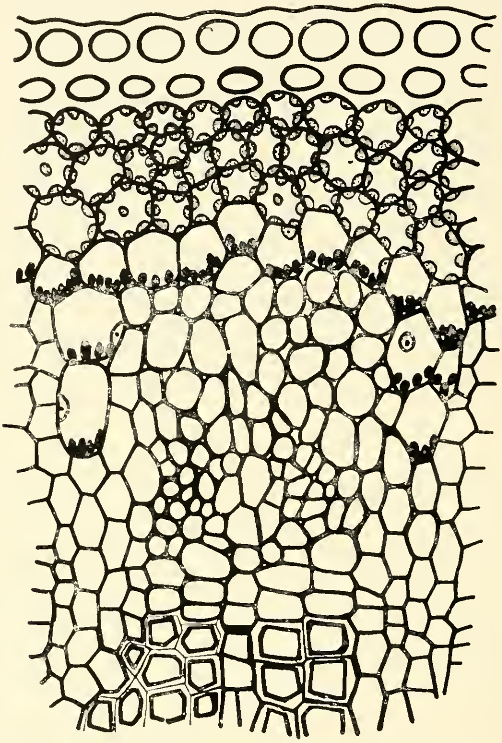


FIG. 869.—*Linum perenne.* Part of a transverse section through a horizontally placed stem showing the starch grains in the starch sheath lying on the lower walls of the cells. (*After Haberlandt.*)

Cases also occur where the starch sheath is dissected into separate arcs or strands, divided by ordinary parenchyma, as in the Nettle and at the nodes of Grasses.

These large starch grains are movable, sinking always to the lowest side of the cell vacuole, and they have been called **statoliths** (Fig. 869), and assigned a function in connection with geotropism (see Volume III).

In underground stems of Monocotyledons, such as *Convallaria*, there is a pronounced endodermis, which may be double or even triple. In the aerial stems, however, the boundary of the stele is usually a sclerotic or collenchymatous zone which grades insensibly into the cortex.

It is evident that the stelar sheath in the stem is by no means uniform, and Strasburger has coined the useful name **phloeoterma** to apply to the innermost layer of the cortex, which must be recognized to be an important anatomical boundary, whether or not it has the character of a true endodermis.

6. *The Primary Vascular Tissues.* Everything within the endodermis is denominated the **stele.** The question of the applicability of this concept, derived from the study of the stem in the Vascular Cryptogams, to the stems of the Spermatophyta, we have discussed previously. It is at any rate certain that in the absence of an endodermis, and particularly in some Monocotyledons, it is impossible to give it the precise connotation which it has, for example, in the Ferns; but it is a handy descriptive term and we shall continue to apply it, without prejudice, to the complex of tissues lying within the cortex and of which the vascular tissues form so important a part. Its outer boundary is usually called the **pericycle.**

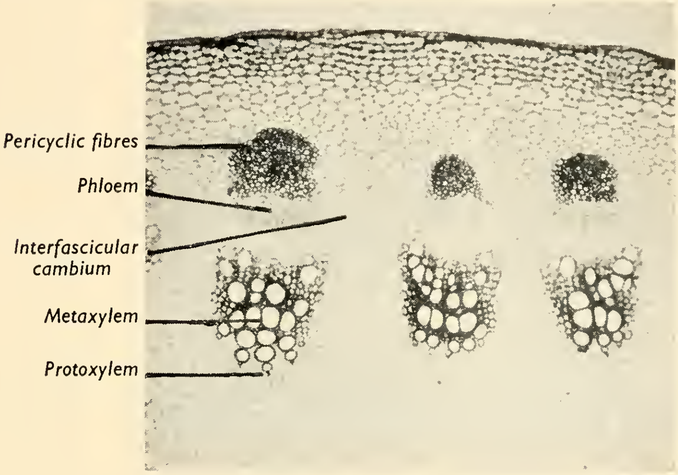
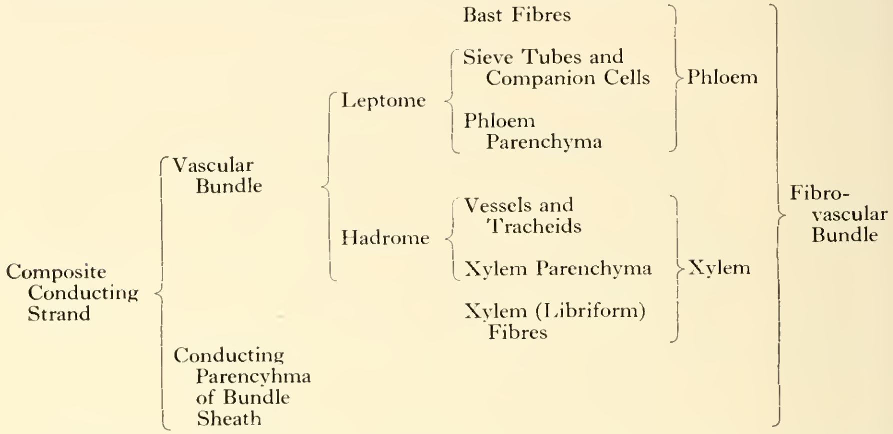


FIG. 870.—*Helianthus rigidus.* Transverse section of stem showing isolated groups of pericyclic fibres opposite the primary vascular bundles.

The pericycle in the stem is very different from the meristematic zone which goes by the same name in the root. The idea of a pericycle is that of a cell layer formed from the outer zone of the procambium, within the endodermis and immediately surrounding the phloem. This position in the stems of Dicotyledons is often occupied by a zone of sclerotic fibres or of sclereids, sometimes continuous, sometimes broken up into groups which lie outside the vascular bundles (Fig. 870). At the present day it is doubtful whether this fibrous zone is really distinct in all cases from the phloem, for it has been shown that it may arise from protophloem in which the sieve tubes and other soft elements have been obliterated and only phloem fibres remain. Whether this is always so cannot yet be stated. The vascular bundles of Monocotyledons, whether they have an individual endodermis or not, are frequently surrounded by sclerotic sheaths, complete or partial, which are quite independent of the phloem but are otherwise analogous to the general pericyclic fibre-sheath in Dicotyledons. It is difficult to see why both types of sheath should not be classed under the same name, as the bundle sheaths in Monocotyledons are particularly characteristic of those stems in which no general pericycle exists.

Each **vascular bundle** is a complex of tissues, partly conducting elements, partly storage elements and partly strengthening elements.

Haberlandt gives the following analysis of the components :—



While **xylem** and **phloem** denote the whole of the two main tissue systems in the bundle, Haberlandt applies the terms **hadrome** and **leptome** to the two sets of conducting elements respectively, to distinguish them from the fibres present.

The most general arrangement of tissues in the bundle is the **collateral**, in which both tissues lie on the same radius, the phloem constituting approximately the outer half of each bundle and the xylem the inner half. We have described above the first appearance of protoxylem at the inner side of the procambial strand and of protophloem at the outer side. The further differentiation of each tissue from procambial cells is centrifugal in the case of the xylem and centripetal in the phloem. In Monocotyledons generally, and in some reduced herbaceous types among the Dicotyledons, the whole of the procambium is thus differentiated and no further addition of vascular tissue is possible. Such bundles are called " closed." Among Dicotyledons, however, it is usual for a zone of cells about half-way across the procambium to become **cambium**, which remains meristematic and thereafter adds cells continuously to both xylem and phloem in radial files. This change marks the beginning of what is called **secondary thickening**. As we have previously pointed out, the organization of cambium may begin so early that every part of the vascular tissue is formed from it (*e.g.*, *Helianthus*), and the radial arrangement rules from the beginning. Such cases show that a clear distinction of primary, or procambial growth, from secondary, or cambial growth, is not always possible.

Even in plants with a meristematic ring which gives rise to a woody stem, differentiation normally begins at a number of separate points on the ring, so that separate primary bundles are for a short time distinguishable. The few exceptions, such as *Vinca* (Fig. 871), in which a continuous ring of xylem is present from the beginning, may really be analyzed into a ring consisting of a very large number of uniseriate bundles, placed very close together and showing a radial arrangement of the elements from the start.

The residual meristem between the original bundles may organize directly into **interfascicular cambium,** continuous with that in the bundles, or it may differentiate into parenchyma. In the first case secondary xylem and phloem are differentiated in the spaces between the original bundles and secondary growth goes forward both in the bundles and between them, forming continuous zones of xylem and of phloem, as in timber trees. In the second case a layer of the interfascicular parenchyma may later differentiate into cambium, but such secondary cambium forms only or mainly parenchyma, and the original bundles remain permanently distinct, *i.e.*, secondary vascular tissue is confined to the bundles. This is not uncommon in woody climbers like the Vine. On the other hand, the spaces between the bundles may remain permanently parenchymatous, with no interfascicular cambium at all, and secondary growth of the bundles themselves is very limited. This is the extreme herbaceous type of stem (see p. 856).

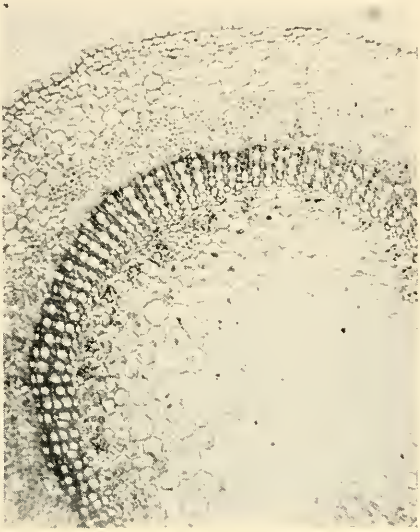


FIG. 871.—*Vinca major.* Transverse section of stem showing continuous zone of xylem.

The parenchymatous intervals between the original bundles are the **primary medullary rays.** They are usually broad at first, and in stems of the Vine type they grow radially by additions from the interfascicular cambium, so that they retain their initial breadth permanently, but in timber trees the original broad rays are soon bridged and closed by the interfascicular xylem. Certain interfascicular cambial cells, however, produce only parenchyma cells, both inwards and outwards, so that at these places narrow rays are built up, which may be uniseriate, or at most two to three cells broad. These narrow rays continue outwards through the whole zone of vascular tissue, no matter how broad it may become, from the pith to the pericycle, interrupted only by the cambium itself.

Medullary rays which originate after secondary thickening has begun are called **secondary rays**. Their point of origin is an initial parenchymatous cell, cut off, usually terminally, from one of the fusiform cambial cells.

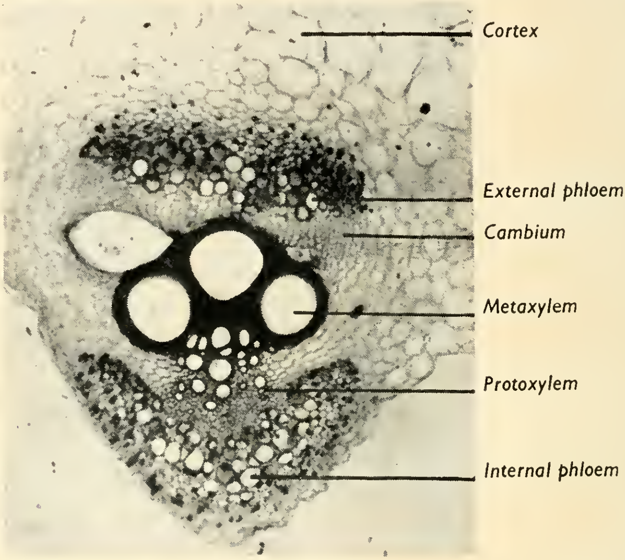


Fig. 872.—*Cucurbita pepo.* Transverse section of a bicollateral primary bundle of the stem. The inner side of the bundle is bounded by the space left after the disappearance of the pith.

Similar narrow rays are formed in the original bundles as soon as radial growth from a cambium is established, and they may be similarly permanent.

The details of secondary growth we will leave until later, while we consider some characters of the individual bundles.

Two types besides the simple collateral bundle deserve mention. The first is the **bicollateral,** in which there is a second phloem region, usually smaller than the first, inside the xylem zone (Fig. 872). This internal or **medullary phloem** may be confined to the primary bundles, or it may develop in the interfascicular region as well, so that a more or less continuous zone of internal phloem results (Figs. 873 and 874). It is a character found

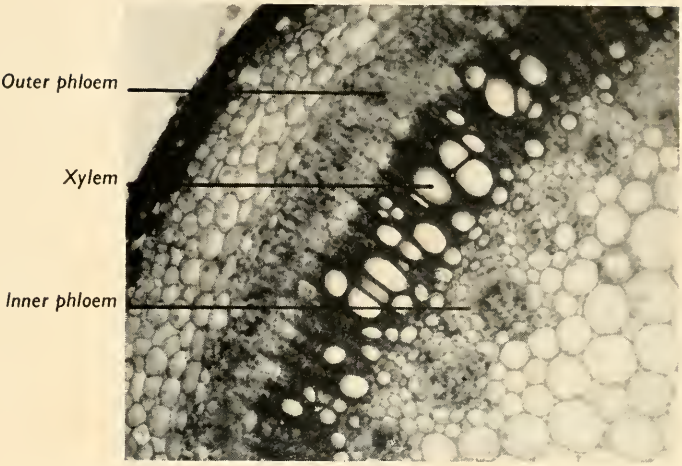


FIG. 873.—*Atropa belladonna.* Transverse section of stem showing groups of phloem elements at the margin of the pith.

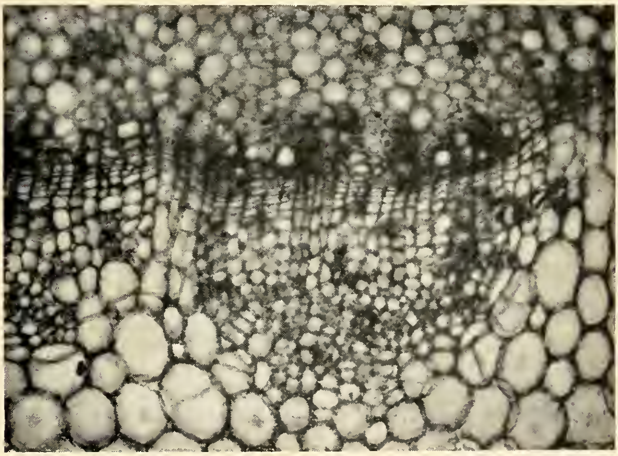


FIG. 874.—*Tecoma radicans.* Transverse section of the stem showing anomalous cambium inside the protoxylems, producing conspicuous wedges of medullary phloem.

only in certain families (*e.g.*, Cucurbitaceae and Solanaceae), sometimes in members with all types of growth, sometimes only in climbing species of the family.

The second type is the **centric bundle** (Fig. 875). This is usually, though not invariably, a closed bundle and is commoner in Monocotyledons, especially in the underground stems, than in Dicotyledons. It may have the xylem in the centre and the phloem outside in which case it is called **periphloic** or **amphiphloic**, or else the reverse when it becomes **perixylic** or **amphixylic**.

The closed bundle which is characteristic of the aerial stems in Monocotyledons is small and has relatively few elements. It is sometimes described as the Y-type from the characteristic grouping of the xylem elements. The protoxylem, which is often crushed and obsolete at maturity, occupies the tail of the Y, and the arms are formed by, or end in, two very large vessels, between which lies a group of small lignified tracheids. Above this is the compact phloem, consisting of regularly arranged sieve tubes and companion cells with a few parenchyma cells at the sides. Another monocotyledonous type has a still simpler xylem, formed of one or two narrow protoxylem elements and one extremely large vessel in the centre of the bundle. This type of bundle is formed mostly in monaxial Monocotyledons with very large, rapidly growing leaves, *e.g.*, Banana, and the extra large vessels are probably correlated with the need for quick development of the water-conducting capacity of the stem. The concentric type of bundle is considered to be the most advanced type in the Monocotyledons and has probably been derived from one of the collateral types.

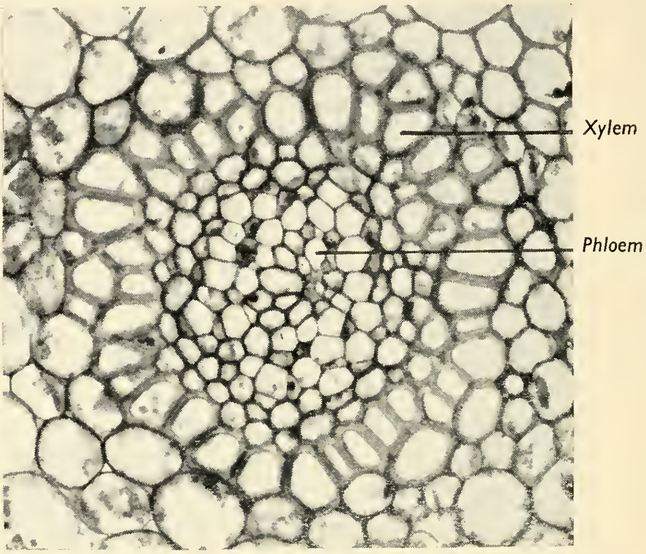


FIG. 875.—*Convallaria majalis.* Transverse section of a single centric vascular bundle from the rhizome showing phloem surrounded by a ring of xylem.

As is well known, the arrangement of the vascular bundles in Dicotyledons is typically in a single, wide ring, while in Monocotyledons they are typically dispersed, seemingly at random, across the transverse section of the stem. In the Dicotyledon the orientation of the vascular tissues is constantly with the protoxylem innermost (the endarch position), but in Monocotyledons, although the general tendency is the same, there is less uniformity, especially in the bundles near the centre.

The parenchymatous tissue enclosed by the ring of bundles in Dicotyledons is the **medulla** or **pith,** but in monocotyledonous stems there is no corresponding region, and the parenchyma among the bundles is generally known as the **ground tissue** or **conjunctive tissue.**

Departures from these typical arrangements will be dealt with later. We must now consider the bundle systems in three dimensions in order to get some idea of vascular architecture.

In Dicotyledons the leaves have usually a narrow base of insertion on the stem. The number of **leaf traces** is therefore nearly always small and may be only one. These traces differentiate downwards from the leaf base and intercalate themselves between the traces of lower leaves (Fig. 876). In this way the trace of a young leaf may reach downwards through several internodes. Eventually, however, at a node, it either becomes united laterally to the adjacent bundle in the ring, or it forks and unites to the bundles on each side of it, producing "synthetic" bundles. The distance it reaches downwards before this happens depends on the leaf arrangement on the stem, since it appears that the traces to which a given leaf unites itself are those of the leaf vertically below it in the leaf spiral. At every node some anastomosis of traces takes place, so that there is at these levels a considerable amount of vascular linkage, while in the internodes the bundles remain separate.

Fig. 876.—*Vicia faba.* Portion of a stem including a node cleared in lactic acid to show the course of vascular bundles. Trace bundles pass out into the petiole and axillary shoots on the right.

The lateral traces of the leaf, where such exist, are close to the median trace at the leaf base, but as they go downwards they are separated by the intercalation of traces from higher leaves, until they may lie far apart. Where there are several traces to each leaf they will thus come to be spaced out where they enter the ring, and in types with many traces, such as *Liriodendron*, they may occupy points all round the ring before they finally join the ring bundles. The lateral traces join the ring at a higher level than the median trace, which means, in terms of apical development, that they do not differentiate until several plastochrons later than the median trace, which is always the strongest and largest and goes farthest down the stem. While the trace differentiates downwards, the period of growth available for differentiation gets shorter in each successive internode and the trace will therefore contain less and less primary xylem and more and more secondary xylem, until it is finally merged in the general mass of secondary xylem. The phloem generally accompanies the xylem, though peripheral portions of phloem may branch off independently and join up with others far above the level at which the trace as a whole finally joins a synthetic bundle.

Comparative studies give good grounds for the opinion that the primitive leaf trace system in Dicotyledons is one with three trace bundles leaving three separate gaps in the vascular ring of the stem, the so-called **trilacunar** type. Reduction to one is due in some cases to abortion of the lateral traces, in others to fusion into one, which, however, may be three-lobed at the base. The many-bundled type of trace is also derivative from the three-trace type, which is frequently found in the seedlings and youngest leaves of plants with complex traces. Even in Monocotyledons the three-trace type is found in many small and slender species and in the young leaves of others, and it appears to be primitive in this group also.

In Monocotyledons the leaf base is broad and surrounds the stem, even in the embryonic state. It may contain thirty to forty trace bundles, which enter the stem simultaneously all round the periphery. Each leaf primordium is quickly pushed outwards away from the apex by the new encircling primordia which follow it, with the consequence that its traces become acutely flexed at the node, bending outwards from a central position into the leaf base (Fig. 877). In Monocotyledons with extended internodes the bundles follow a course downwards which is similar to that in Dicotyledons, tending gradually outwards towards the point of anastomosis with older bundles, which appear to be usually those of the next leaf vertically below the leaf considered, *i.e.*, on the same orthostichy (see Chapter XXII). At the nodes the number of anastomosing bundles is so great that it creates a nodal plexus of intermingled bundles which may extend right across the stem, and is increased by the insertion of numerous traces from the axillary buds.

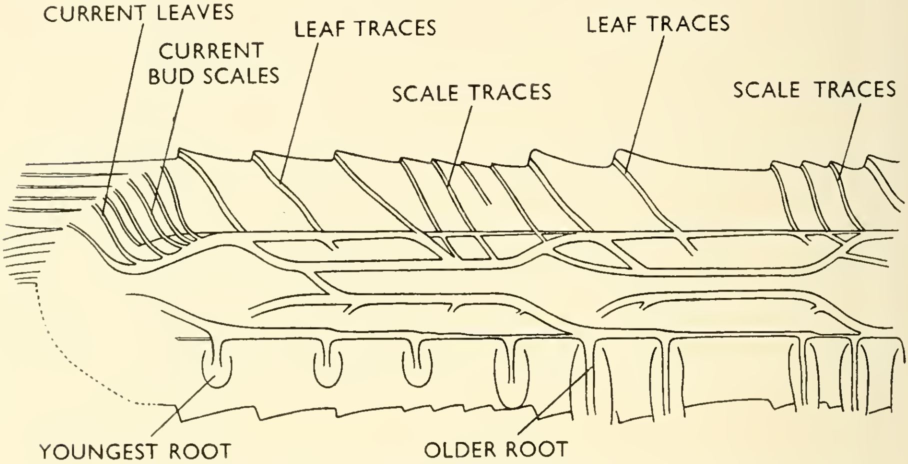


FIG. 877.—*Convallaria majalis.* Diagram illustrating the course of vascular bundles in the rhizome. (*After Euker.*)

It must be admitted that the course of the bundles in even a simple Monocotyledon is not yet known with sufficient accuracy to warrant positive statements, while in those species with contracted stems the complexity and irregularity defies analysis. The whole question of vascular development is indeed in a somewhat hazy state. For example, although basipetal differentiation of vascular elements within the procambium seems to be the rule, it is by no means certain that the differentiation of the procambium itself, from the primary meristem, is not acropetal or continuous. The above account must therefore be regarded as provisional.

The development of the meristematic cells in a young leaf axil into an axillary bud complicates the dicolytedonous nodal structure further by its special system of traces. The axillary bud has an apex which is a miniature of the main apex and has the same procambial arrangement, giving rise to a duplicate of the stem stele. As this differentiates downwards into the stem, the ring or group of traces opens out fanwise, forming two bundles which pass into the main ring between the bundles which flank the median leaf gap and join them above the level at which the median trace of the subtending leaf itself joins an older trace in the ring.

Exogenous adventitious buds such as those on the corms of *Cyclamen* are apparently connected secondarily to the stele of the parent stem. Procambial strands come from the bud and differentiate inwards through the cortex towards the stele, and the formation of vascular tissue in this procambium is likewise downwards from the bud.

7. *The Cambium.* It has been previously pointed out that the organization of cambium from procambium marks the beginning of radial growth, commonly called secondary growth, which is capable of indefinite expansion outwards and will, if continued, build up a massive woody stem.

In many herbaceous stems, although secondary growth begins as in woody plants, it does not continue beyond one year. The structure of such herbaceous stems is therefore similar to that in the one-year-old stems of woody plants.

The **cambial initials** are distinguished in the procambium by their repeated tangential, longitudinal divisions, giving rise to a zone of cells which appear narrow in transverse section. This occurs in the part of the stem apex where active growth is still going on, and the cambial initials undergo considerable elongation and become radially compressed by the expanding tissues of the pith and cortex. In spite of these changes the cambial cell remains a true meristematic cell, and its repeated tangential divisions cut off new xylem cells centripetally and new phloem cells centrifugally. It is difficult to distinguish these new tissue elements in their early stages of development from the true cambial cells, and it is not possible to say in every case whether the fully developed cambium consists of only one layer of cells or of more.

The position at which the cambium forms in the procambium may be physically determined by the gradient between acid sap from the differentiating wood and alkaline sap from the phloem. This theory, which is due to Priestley, maintains that the cambial layer lies at the *p*H on the gradient which corresponds to the mean isoelectric point of the cell proteins (about *p*H 4·5), and that the protoplasm of the cambial cells remains unvacuolated because at the isoelectric point colloids have their minimum affinity for water and their maximum density.

The same theory extends to the formation of interfascicular cambium from fully differentiated parenchyma cells and perhaps also to the appearance of the phellogen. Both these changes involve the alteration of cells with large vacuoles and little protoplasm into meristematic cells which have no vacuoles and abundant protoplasm. The isoelectric point of the cell proteins is the condition which would seem most favourable to such a change. The cambium does in fact lie between acid xylem (*p*H 3·4 to 5·0) and alkaline phloem (*p*H 7·8), while the phellogen lies between the strongly acid cork (*p*H 3·0) and the less acid cortex (*p*H 5·5 to 6·5).

Protoplasm at its isoelectric point will lose water to vacuolating cells and the condensed non-vacuolate condition produced is that most favourable to protein synthesis.

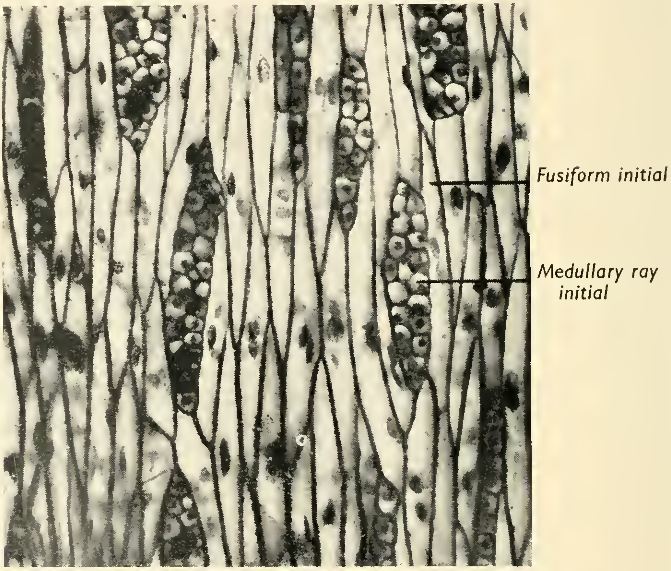


FIG. 878.—*Ulmus procera.* Tangential view of the cambium in a woody stem showing elongated cambial elements and embryonic medullary rays.

When cambium is viewed in tangential longitudinal section, two types of cell are seen, the long, pointed fusiform cells which give rise to the vascular elements, and the small, isodiametric cells in groups, which produce the medullary rays (Fig. 878). These latter are much more numerous than in Conifers and may account for up to 55 per cent. of the cells in a cambial ring. The long, fusiform elements are thin walled and without pits except in the dormant season. They are often flexed into curves as they pass round the groups of ray cells. Their divisions are mostly longitudinal-tangential, and it is doubtful whether they divide radially. More probably the appearance of radial division is created by transverse walls which become more and more inclined in a tangential direction until they are vertical, thus increasing the number of cells in the ring, as it expands with growth. In radial section the long cells are very narrow, with chisel edges at both ends, which overlap those of the next cells above and below. This overlapping of the cell ends has been attributed to "sliding growth," in which the walls of neighbouring cells actually slip along each other, but this is doubtful, for many reasons, and it seems more probable that it is produced by local growth of the young, plastic cell-walls, above and below each new transverse division wall, at opposite ends respectively, in such a way that the transverse wall is tipped into the vertical without any mutual slipping of the cells. The cambial ray cells, on the contrary, divide in all three planes.

Bailey has shown that in Dicotyledons there are three main types of cambium, corresponding to three types of wood structure.

1. Initial cells averaging 890 microns in length, producing long, narrow vessel segments with scalariform pitting of the end walls.
2. Initial cells averaging 410 microns, producing short, broad vessel segments with cross walls which are simply pitted or else absent.
3. Initial cells averaging 250 microns, producing vessels similar to type 2, but the cambial cells are arranged in regular horizontal rows ("Etagen cambium") and give rise to a corresponding "storied" structure in the wood.

These three types are regarded as marking advancement in specialization of the vascular structure.

The cambium in the resting state, in winter, is sharply marked off from the vascular tissues, with fully formed vessels and sieve tubes lying in immediate contact with the cambial cells from which they have been formed. During the summer activity, however, the cambial zone seems much broader and less clearly delimited, because tangential divisions follow one another so rapidly that the true cambial zone is flanked on both sides by a layer of still undifferentiated cells, and the transition to the mature vascular elements is thus spread over a broader zone of development.

It has been shown that the cambial growth in spring begins in the swelling buds and spreads downwards from them. It begins simultaneously all over the tree, but the rate of spread is much slower in the older branches and it stops sooner in them than in the young shoots. There is good evidence that the stimulus to cambial growth is the diffusion of hormones from the leaf initials in the bud. Auxin-a and heterauxin (see Volume III) can both start strong cambial growth when they are supplied to a shoot, and auxin has been found in naturally active cambium and is known to be produced by leaf initials. This direct relation of leaf development to cambial activity is probably the reason for the proportionality between the extent of leaf surface and the amount of vascular tissue formed in the stem, which observation has revealed. The hormone explanation may hold good not only in the growth of the normal cambium but in the differentiation of new vascular tissue from old permanent tissues, which occurs in regeneration growth after wounding. Such new developments show a definite directional guidance from point to point, often around obstacles, which strongly suggests the action of a diffusing hormone. This is also probably true of new, adventitious, vascular differentiation, as in the case of *Cyclamen* (see p. 891).

The cambium, like other meristematic tissues, does not itself undergo any marked change throughout its existence. The only visible indication of age is a gradual increase of the average length of the cambial cells and of the tracheids formed from them, an increase which may continue for a number of years from the beginning of cambial growth. Eventually, however, a steady state is reached and no further change in length occurs.

In the most pronouncedly herbaceous plants there may be no interfascicular cambium, and the separate bundles themselves have little or no cambial growth, while in the most extreme herbaceous types there is not even a continuous ring of procambium. Indeed the annual, monocarpic habit of growth, limited to a single growing season, is probably brought about by the absence or early disappearance of cambium and the consequent lack of the power of extended growth.

Monocotyledons are generally supposed to have no cambium in their bundles, but the metaxylem elements are often in radial rows, which is characteristic of cambial growth, and they probably resemble the annual Dicotyledons in having cambia that are very short lived. The specialized cambia of some Monocotyledons which undergo secondary thickening are dealt with on page 912.

In connection with the cambium we may briefly mention .the abnormal tissue formation known as **callus,** which is associated with wounds and similar injuries. The name is applied to irregular tumour-like outgrowths, due to a resumption of meristematic activity called out by the injury. Any living tissue may contribute to this development, but where the cambium is involved, its contribution is much the greatest. Thus a callus ring arises on the cut ends of branches or old roots, which is almost entirely due to growth from the exposed end of the cambium and which spreads until the wounded surface is completely covered. This new tissue is almost entirely parenchymatous, and there is no regular differentiation of tissues, as in normal cambial growth. At the most a few irregular scattered tracheids or sclereids may be formed, embedded in the mass, while the outermost cells may become corky.

8. *Secondary Vascular Tissues : Phloem.* The **metaphloem,** including the secondary phloem, if any, consists of sieve tubes, their companion cells and phloem parenchyma. The companion cells, originally sister cells of the sieve tube cells, usually divide transversely more than once, so that they are individually much shorter than the sieve tube segments. The phloem parenchyma cells are variously shaped, and may be so long and narrow that they scarcely justify their name.

Mingled with these elements in many plants are phloem fibres, either scattered or, as in *Tilia* (Fig. 879), in tangential bands alternating with the conducting tissues. These fibres closely resemble those which form the fibres of the so-called pericycle, external to the phloem, and are often classed with them as **libriform fibres,** from the old name " liber " (or " bast "), applied to the inner bark, in which the phloem was distinguished as " soft bast " and the fibres as " hard bast." Fibres of the secondary phloem, being produced from the cambium, show the same radial arrangement as other phloem cells, but the pericycle fibres, coming direct from procambial cells, do not.

Libriform fibres are narrow and very highly thickened, and their pits are very small, so that the pit opening shows little or no border. The pit openings are slit-like and the openings on the inside and the outside of the wall are usually at right angles to each other, so that the pits appear like minute crosses on the cell wall. They are longer than the xylem fibres, but flexible and tough rather than brittle. Jute, and several other important fibres consist of this type of cell.

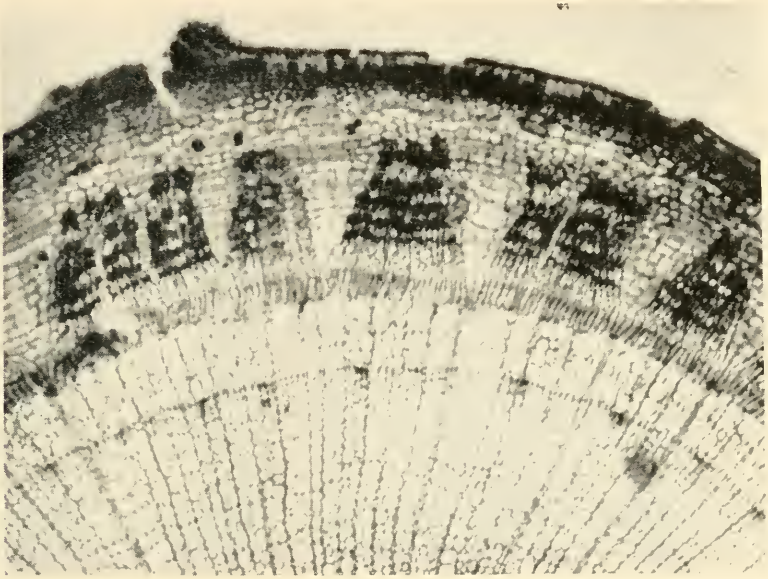


FIG. 879.—*Tilia vulgaris.* Transverse section of a woody stem showing wedge-shaped medullary rays in the phloem zone and phloem composed of alternating tangential bands of sieve tubes and thick-walled phloem fibres.

9. *Secondary Vascular Tissue: Xylem.* The term **metaxylem** includes all the secondary xylem. The cell structure of secondary xylem is very variable, and each type of wood has its recognizable characteristics, by which it may be identified. The usual constituents are vessels or tracheae, tracheids, xylem parenchyma and fibres of various types.

In true vessels the successive elements open into one another in longitudinal succession by membraneless portals so that the lumen forms a continuous passage. This involves the alteration or disappearance of the transverse walls which separate the young elements from each other.

Comparative studies have shown that in the wood of certain families which are predominantly arboreal in habit the vessel elements are narrow and long and have steeply oblique end walls with numerous scalariform perforations (Fig. 880). In this they resemble the vessels of the Gnetales. Examples are : *Magnolia*, *Betula*, *Salix*, *Myrica*. From this unspecialized condition there has been a progression towards vessels with short elements, as broad as or broader than their length, and with transverse end walls which have either one very large central perforation, or are, in the final stage, completely absorbed, leaving only a ring on the vessel wall to mark where they had been. Examples of this are common among herbaceous plants (Fig. 880).

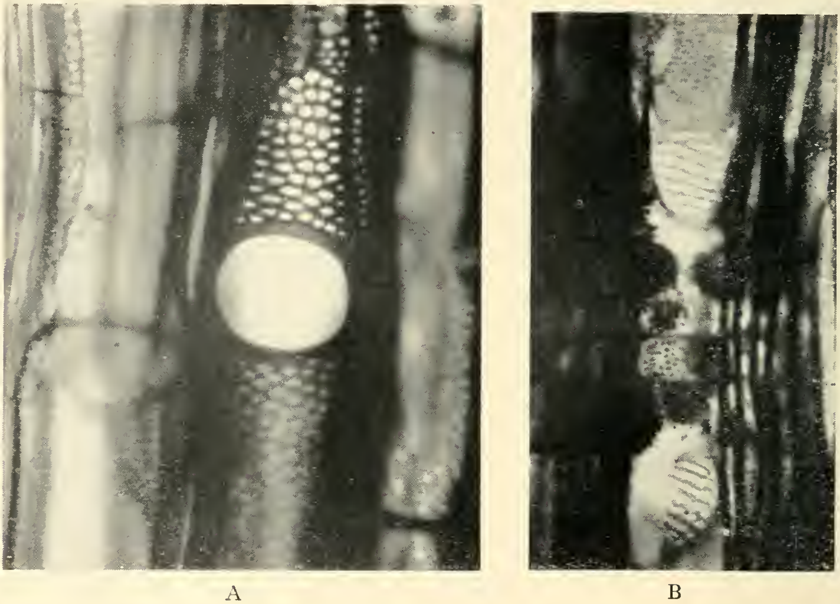


Fig. 880.—Comparison of terminal perforations in vessel elements.

A, *Helianthus annuus*. Open pore. B, *Salix caprea*. Scalariform.

The lateral walls of vessels in the secondary wood may bear pits which are either scalariform or circular, the latter being either side by side or alternating with each other. Spiral vessels also occur in the wood of many families, but not in those which are regarded as being the most primitive.

Movement of water upwards in the xylem under the influence of transpiration tension follows the lines of least resistance and large, fully open tubes must obviously afford an easier passage than narrow elements with many cross walls, even if the latter are perforated.

Climbing plants which have very long, narrow stems are those in which the resistance to hydraulic flow is greatest, and they are notable for the large average diameter of their vessels. Poiseuille's Law of fluid flow expresses the velocity thus:—

$$V=\frac{\pi p r^4}{8 l \eta},$$

where V = velocity of flow.
p = pressure difference.
r = radius of tube.
l = length of tube.
η = coefficient of fluid viscosity.

The velocity is directly proportional to the fourth power of the radius and inversely proportional to the length of the path of flow. Velocity is thus much more sensitive to differences of radius than of length, and the resistance offered by a long stem can be readily compensated by the increased width of the vessels. To double the radius of a vessel will increase the flow capacity by sixteen times, but to halve the length of the path will only increase the flow twice.

Owing to the irregularities of their structure the vessels may have a conducting capacity which is no more than 30 to 40 per cent. of the theoretical efficiency but their comparative capacity is nevertheless governed by the hydraulic laws.

The flow of water upwards proceeds through very numerous fine channels, branching and rejoining, which are formed of single vessels or of small groups of vessels islanded among tracts of non-conducting parenchyma and fibre cells. Among herbaceous plants the leaf trace bundles serve for conduction only to the leaves to which they are connected, and there is some evidence that this physiological segregation may persist downwards in the synthetic bundles of the lower stem. Whether this applies to the massive secondary wood in trees is doubtful. There is no positive evidence of the anatomical segregation in the mass of wood of distinct conducting tracts associated with individual branches. The selective flow through limited channels, which may be observed when a single leaf or branch draws a coloured solution through the main stem, is probably conditioned by the downward transmission of the water tension, which is the motive force of the flow, through the physically most direct path available.

Vessels anastomose freely both tangentially and radially, so that the water currents, even if confined to the vessels, may shift their paths readily in either direction, even from one annual ring to another. The force of transpiration is not, however, sufficient to draw water across the medullary rays, in the absence of a vascular connection.

In most woody plants the vessels only remain functional for, at most, a few years after their formation, and frequently only for one year. The outermost annual rings of wood are often lighter in colour and softer in texture than the older wood. They form the **alburnum** or sap wood, while the older rings compose the **duramen** or heart wood (Fig. 881). Only the outermost portions of the sap wood may be active in conducting water, and the heart wood takes no part whatever in conduction. Water storage in the duramen is confined to the living cells of the medullary rays and xylem parenchyma, but as the conducting elements pass out of action they are often filled with resinous or gummy substances and tannins, and the walls may be impregnated with colouring matters, an example of which is Haematoxylin, which oxidizes to the well-known dye, Logwood. Mineral substances, such as Calcium carbonate in *Fagus* and *Ulmus*, Silica in *Tectona grandis* (Teak) or Calcium oxalate in *Chloroxylon* (Satinwood) may also impregnate the heart wood, adding greatly to its weight and durability and enhancing its value as a strong core in the tree trunk.

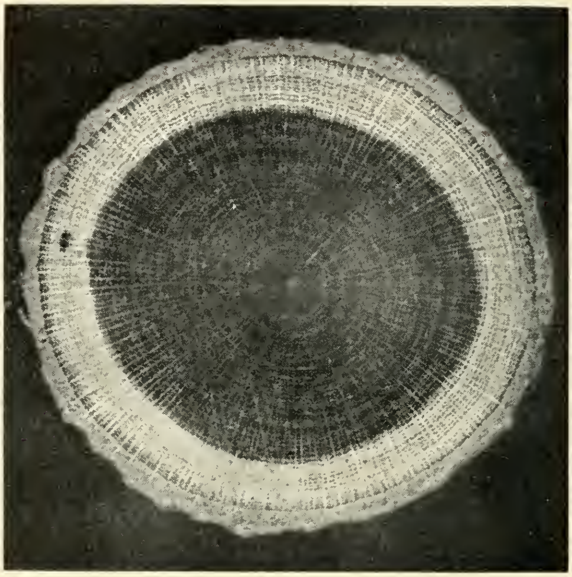


FIG. 881.—*Laburnum anagyroides.* Transverse section of a woody stem showing alburnum and duramen traversed by light-coloured medullary rays.

Vessels which are passing out of action often become partially or wholly filled by sac-like ingrowths from the living parenchyma cells which are in contact with them. The pits between parenchyma and vessels are not bordered on the side of the former, so that they present a large surface of pit membrane, which is expanded by turgor pressure into the cavity of the vessel. Such ingrowths are called **tyloses** (Fig. 882). They are balloon-like, cylindrical or even branched, and have thin walls, but occasionally they may be lignified, either like stone cells or like the walls of the vessel in which they lie. What determines these differences is unknown.

The young vessel elements usually expand laterally very rapidly, reaching their full diameter even while still in contact with the cambium, and creating considerable tissue pressures, while tracheids do not thus expand ; yet there is no invariable distinction of size, though normally the expanded vessels are larger than the tracheids of the same wood. While vessels are normally the channels of long distance transport, tracheids serve chiefly for short distances and for water storage. Offshoots of the main bundles, including the leaf traces and the leaf veins, consist almost entirely of tracheids. This distinction of function implies an advanced state of specialization and is characteristic of the Dicotyledons.

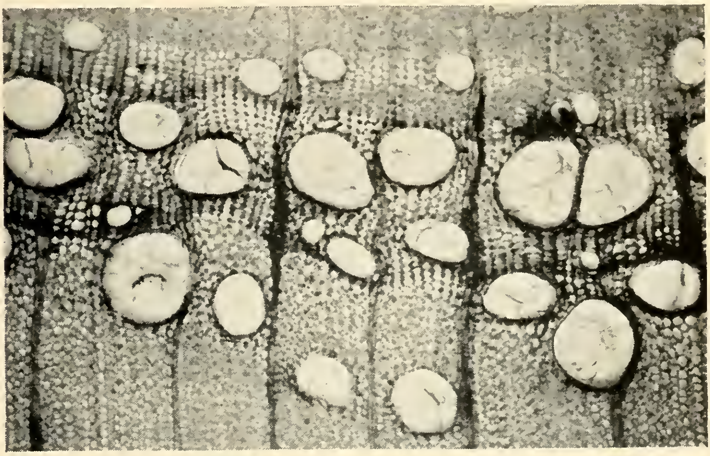


FIG. 882.—*Robinia pseudacacia.* Transverse section of a portion of secondary wood showing large vessels filled with thin-walled tyloses.

Fibres play a large part in the make up of the secondary wood (Fig. 883). Firstly there are the **fibre-tracheids,** thicker walled than the true tracheids but with the same bordered pits, and in some cases not sharply distinguishable. These grade through intermediate elements, increasingly narrow, thick-walled and elongated, to true **libriform fibres.**

Libriform fibres in the wood are often as much as seven times as long as the cambial initials. Measurements show variations between 0·3 and 1·3 mm. Nevertheless this is small compared with the bast-fibres, which are seldom less than 1·0 mm. long and may reach 7·7 mm. in *Urtica* (Nettle), or even 40 cm., *i.e.,* 16 in., in *Boehmeria nivea* (Ramie). In both cases, however, the elongation during differentiation is very considerable. As it takes place in regions where general growth in length has ceased, it has been held that the elongation of the individual cells must imply slipping or sliding of the cells on each other, and this has been called **sliding growth.** The idea is open to some anatomical objections, but it cannot be said that the alternatives suggested are very convincing. One counter-argument, usually regarded as weighty, is that the pits in the walls of adjacent fibres show a normal degree of correspondence, which is considered to be impossible if the walls have slipped during growth. It is not impossible, however, that this correspondence may be secondarily established, since it is also found in the pits between adjacent tyloses in wood vessels, in which case the cells have manifestly only come into contact at a late stage of development.

The last class of fibres is that called **substitute fibres,** which are really living cells, often containing starch, but with lignified walls. They are not clearly separated, except in point of length, from xylem parenchyma, and indeed they are sometimes divided by transverse walls forming a short chain of typical parenchyma.

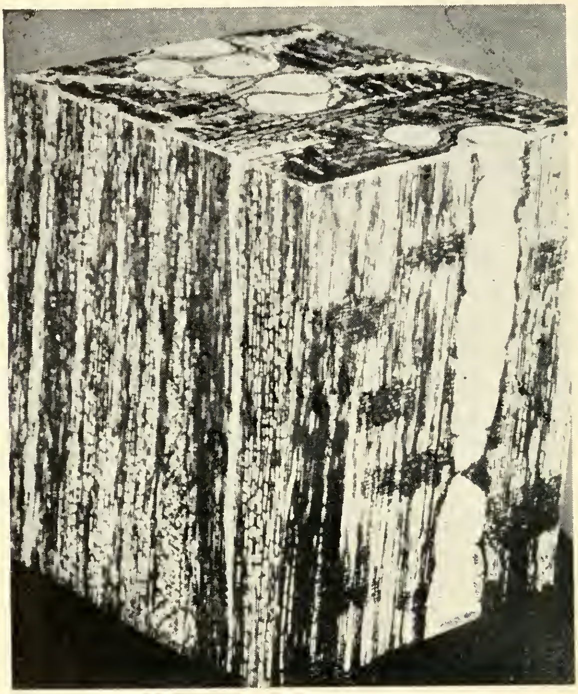


FIG. 883.—*Quercus robur.* Photograph of a model showing a three-dimensional view of the structure of the secondary wood. On the right, longitudinal radial view ; on the left, longitudinal tangential view.

The xylem parenchyma cells arise by repeated transverse divisions of cambial initials. Their walls are lignified but not heavily, and they are richly supplied with simple pits on the radial and horizontal walls. They are important as stores of reserve substances, either starch, in most hard-wooded trees, or oil in soft-wooded trees.

They also form important links between the cells of adjacent medullary rays. Careful investigation shows that they are seldom isolated, but occur in irregular tracts, which contact one or more of the medullary rays, usually two, between which they form a tangential bridge. In this way they serve to make an intercommunicating system of living cells in the wood, providing for tangential transport, as the medullary rays themselves do for radial transport.

The distribution of the xylem parenchyma is highly characteristic of particular species of wood and is one of the features by which they may be identified. There are two main types :—

1. **Apotracheal,** which includes those occurring in tracts which are independent of the vessels, *i.e.*, **metatracheal,** and also the rarer cases where they are diffuse or **dispersed.**
2. **Paratracheal,** which includes all cases where they are grouped around the vessels.

In Conifers the xylem parenchyma usually occur only in the last row of elements in each annual ring. This arrangement, called **terminal,** is very rare in Angiosperms, being known only in *Magnolia* and *Salix*.

10. *The Medullary Rays.* The majority of the medullary rays in secondary wood are uniseriate, that is one cell in breadth as seen in transverse sections of the wood, but broader, **compound rays** occur in some species, while **aggregate rays,** formed by the close grouping of a number of uniseriate rays, also occur, especially in association with leaf or branch gaps in the woody cylinder. All rays which originate from cambial cells are classed as secondary rays, and new rays, intercalated between the previously existing ones, are commenced in each year of growth, so that the total number steadily increases with the age and girth of the tree, the average distance between rays, tangentially. remaining roughly uniform in successive rings of growth. Once a ray has been started it is invariably carried on through all subsequent growth rings. Outside the cambium the ray is continued in the phloem, so that each ray has a xylem and a phloem portion. The ray in the phloem may be both longer and wider than in the xylem and in plants such as *Tilia*, where the phloem rays are V-shaped, the widening is due to serial cell divisions resembling cambial growth.

Medullary ray initials, which are much shorter than other cambial cells, cut off cells both inwards and outwards by successive tangential divisions, though many more are added to the xylem rays than to the phloem rays, corresponding to the more rapid formation of xylem. The cells cut off are directly converted into parenchyma and added to the rays without further divisions. The xylem ray cells become lignified like the other xylem parenchyma, the phloem ray cells are thin-walled and pitted, like phloem parenchyma. During the winter, when the cambium is dormant, the ray initials in the cambium take on the character of phloem ray cells, so that there is then no break in the radial continuity of the two portions of the ray. New initial cells are formed in spring by the tangential division of the innermost phloem ray cell.

Most rays are comparatively short in the vertical direction, some no more than one cell in height, and the tallest are not usually more than twenty cells (Figs. 884 and 885). The cells are, with few exceptions, uniform in character, and all contain living protoplasm, nuclei, and reserves of food material. They remain living without growth or division for as long as the plant exists, and the ray cells of heart wood in old trees are the oldest living

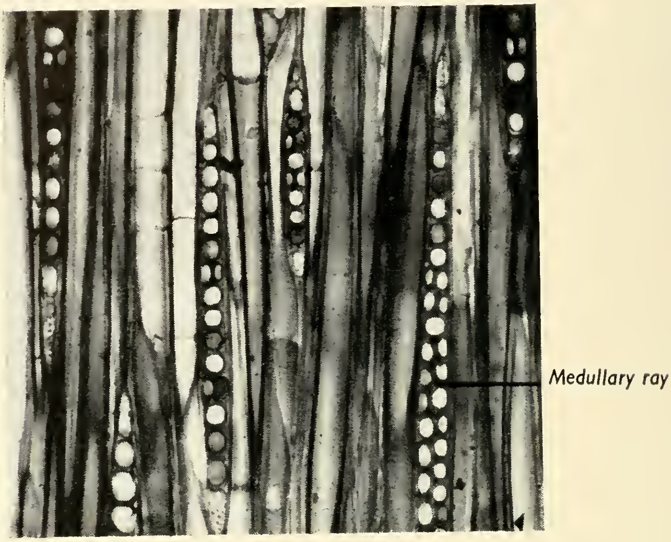


FIG. 884.—*Acer pseudoplatanus.* Longitudinal tangential section showing narrow medullary rays cut transversely.

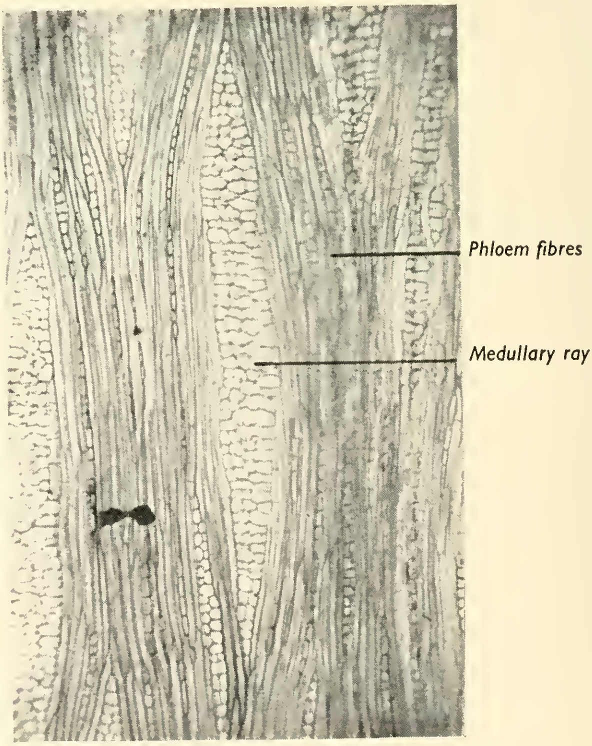


FIG. 885.—*Tilia vulgaris.* Longitudinal tangential section through the phloem zone showing both multiseriate and uniseriate medullary rays.

cells known. They may persist for an indefinite period without growth and without division.

Medullary rays in woody Dicotyledons have been classified into a number of types on the following characters: (1) Whether both uniseriate and multiseriate rays are present, or only one kind. (2) Whether the cells composing the rays are all alike short, or whether some are vertically elongated. The heterogeneous type, with both kinds of rays and both kinds of cells, is regarded as the most primitive, and the homogeneous type with only multiseriate rays of short cells is probably the most advanced.

Where the xylem ray cells abut on vessels, the ray field, *i.e.*, the area of contact between ray cell and vessel, has simple, not bordered pits, which are sometimes single and very large, but more often small and either circular or elliptical (Fig. 886).

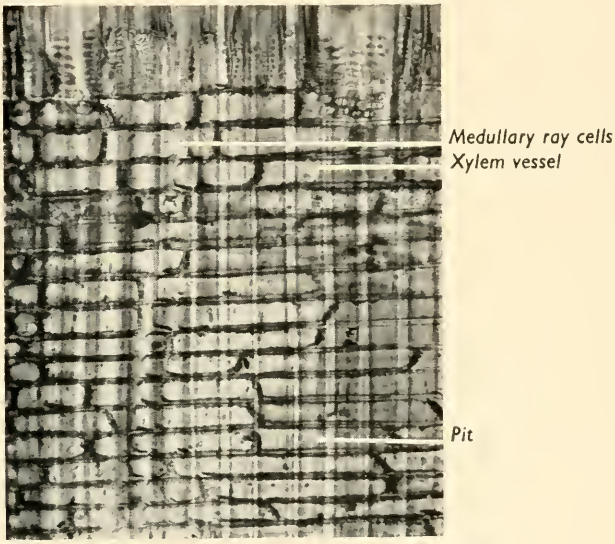


FIG. 886.—*Acer pseudoplatanus.* Longitudinal radial section showing a medullary ray crossing the xylem elements. In some of the ray fields circular pits may be seen.

11. *Types of Wood.* At the resumption of activity in spring the cambium produces comparatively large, thin-walled, rapidly expanding xylem cells, the **spring wood,** which meets the need for active conduction of water to the developing buds. At the height of summer cambial growth is reduced, but it again increases to a secondary maximum in autumn, associated with increased rainfall and an abundance of photosynthetic carbohydrates. The **autumn wood** is, however, much denser than the spring wood and contains a higher percentage of fibres. It is the dense zones of autumn wood which mark the " grain " of commercial timbers.

Tracheids, vessels and fibres may be formed at any time during the year's growth, and the pattern of their distribution is often an index to the identity of the wood and decides its physical characteristics (Figs. 887 and 888). Two alternative patterns affecting the vessels are so well marked that woods may be classified by them at a glance. In one class the formation of vessels is almost or entirely confined to the spring, so that each annual ring begins with a zone of large vessels. This is called **ring-porous** wood (Fig. 889).

In the other class vessels are formed throughout the year. Such wood is called **diffuse-porous** (Fig. 890). The vessels in these woods are nearly always smaller than in the ring-porous type, and are sometimes scarcely broader than the tracheids. They are also apparently much shorter. The total length of the open lumen in a single vessel is difficult to determine, but the passage of coal-gas through the wood gives us some idea of their relative lengths. Wood without vessels is completely impermeable to gas, but it will pass through a 10-ft. length of the ring-porous wood of Ash in sufficient amount to ignite, while more than 2 ft. of the diffuse-porous wood of the Maple stops it completely.

A small group of genera belonging to the order Ranales, namely *Drimys* (Fig. 891), *Trochodendron* and *Tetracentron* (Fig. 892), is notable for having no wood vessels at all. These woods are spoken of as **homoxylous,** for they consist of radially arranged tracheids of uniform width, recalling the wood of *Pinus*. The resemblance is carried further, for they have large bordered pits on the radial walls of the tracheids, like those of Conifers, though the pitting on the spring wood is scalariform. Whether this is significant from the evolutionary standpoint, as indicating a primitive character in these three genera, or whether they have lost their vessels by reduction in the course of evolution is a matter of opinion.

Each year's complement of secondary thickening forms one **annual ring.** The change from the dense, small-celled autumn wood to the soft, open type of spring wood is normally well-marked and unmistakable in all temperate trees, but in trees grown in an equatorial climate growth is continuous and the annual rings may be non-existent. The older fossil woods have either no annual rings or vague rings with no marked break between them, showing that there were no marked seasons even in temperate latitudes in Carboniferous time. A marked differentiation of climate first appears in the Mesozoic period.

Annual rings are an excellent record of climatic variations, being wider or narrower according to the quality of the season and having a reduced average width in high latitudes and at high altitudes. It does not follow, as might be imagined, that narrow rings imply stronger wood. On the contrary, unfavourable conditions limit chiefly the development of the autumn wood, and narrow rings may consist mainly of the spongy spring wood. The width of the annual ring is not uniform all over the tree but is greater in the upper part, associated with a longer period of cambial activity.

Annual rings are usually symmetrical in vertical stems, but in oblique or horizontal branches, especially near the base, they become asymmetrical, the lower half (in Conifers) or the upper half (in most Angiosperms) being

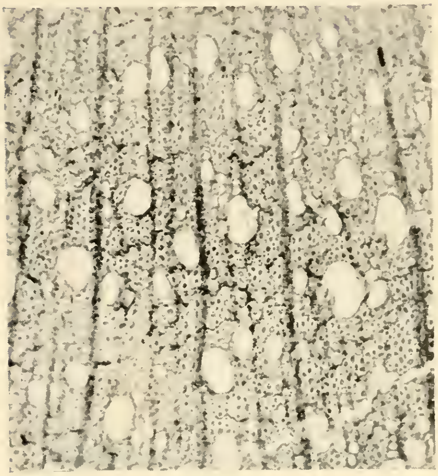


Fig. 887.—*Fuchsia riccartoni.* Dense wood. Transverse section of the secondary wood showing the large proportion of thick-walled fibres.

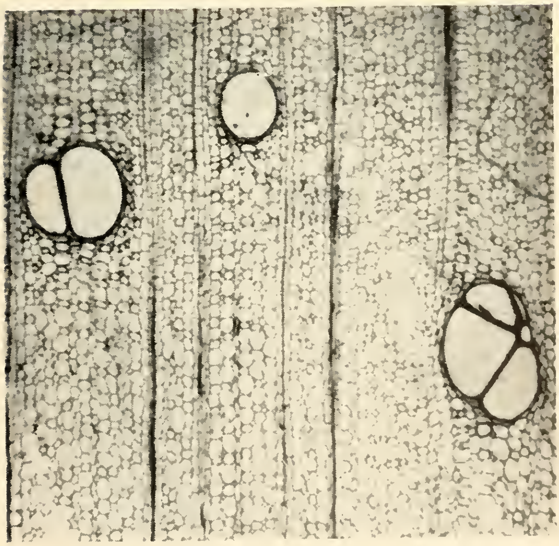


Fig. 888.—*Ochroma lagopus.* Balsa. A light wood. Transverse section of the secondary wood showing the predominance of thin-walled elements.

FIG. 889.—*Fraxinus excelsior.* Ring-porous wood. Transverse section of the secondary wood showing the concentration of vessels at the inner margin of each annual ring.

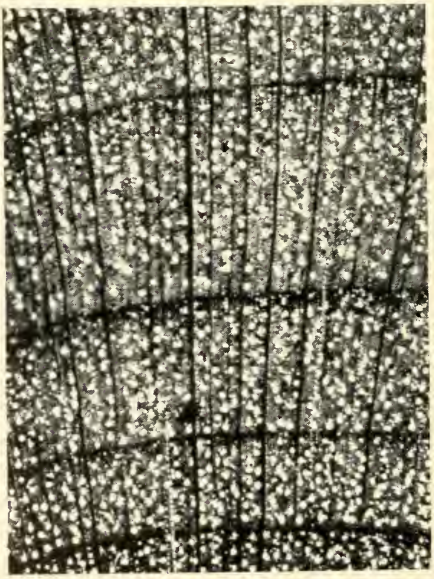


FIG. 890.—*Buxus sempervirens.* Diffuse-porous wood. Transverse section of the secondary wood showing the diffuse distribution of vessels.

thicker than the other and consisting of differently thickened elements. In Conifers the lower wood is reddish, the upper white, the former having much thicker cell walls. The difference is attributed to the mechanical effect of the weight of the branch, the upper wood being called **tension-wood** and the lower portion **compression-wood.** Vertical stems subject to consistent wind pressure from one side may show the same differences.

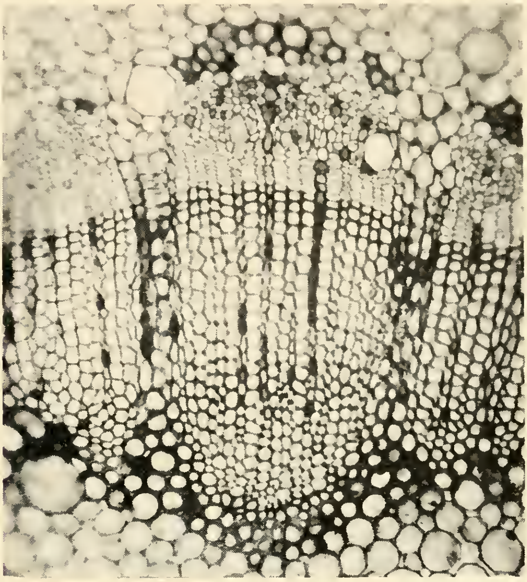


FIG. 891.—*Drimys winteri.* Transverse section through the vascular zone of a stem showing homoxylous wood with no vessels.

Severe frost may cause upward or downward bending of large branches according to whether the thinner-walled tissue lies on the lower or the upper side of the branch, as is remarked in "Lorna Doone."

In the contracted stems of rosette plants successive rings of wood may not be formed at all, or if they are, they are related to environmental conditions, not to age. A constant relation to annual growth is only maintained in main stems of unlimited growth. In short branches, such as fruit spurs, annual rings are only formed in the first few years; while in thorns, unless they bear leaves, there is never more than one ring, however old they may be.

The phloem rarely shows indications of annual rings. The periodicity of cambial growth is less marked on the phloem side. Activity begins later and may, in some cases, continue into and perhaps through the winter, the spring change in the phloem not being the formation of new elements, but the very marked swelling of the old elements through water intake. Towards the end of its life the phloem may, though rarely, become lignified, as may be seen in old stems of the annual Sunflower.

Wood anatomy has proved a very useful adjunct to systematic Botany and is serving to supplement the ideas of classification and evolution based upon external morphology. The features principally used for comparison are: fibre types, distribution of the xylem parenchyma, type of perforation in the end walls of vessels and the presence or absence of "storied structure" in the wood. The origin of storied structure has been explained under the heading of Cambium. It implies a marked uniformity of length in each series of tracheids and vessel elements, as seen in longitudinal section, so that the wood appears to be built up of vertically successive layers, or storeys. These characters are not always sharply marked and a good deal has to be left to the judgment of experience in deciding systematic affinities on wood characters.

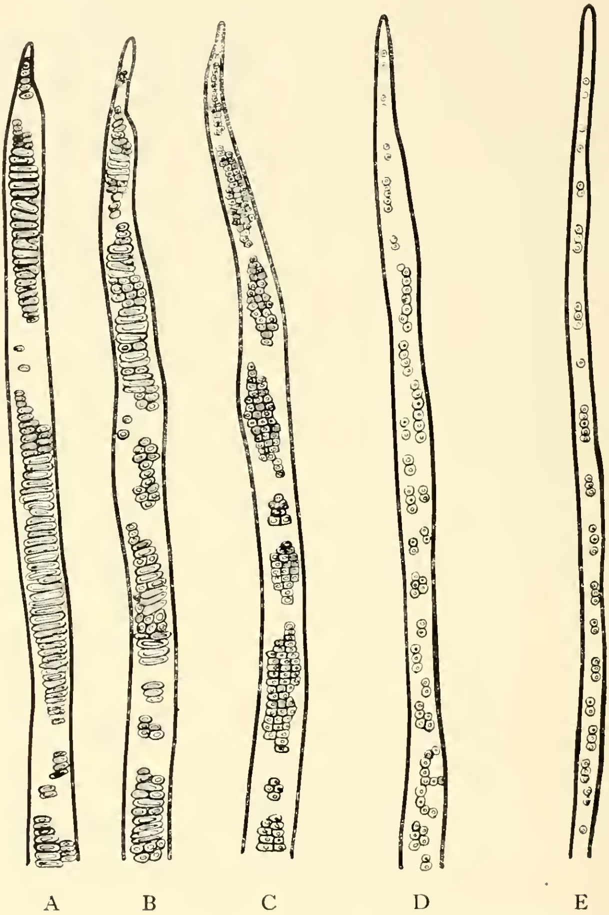


Fig. 892.—Tracheids in homoxylous members of the Ranales, *Tetracentron*, *Trochodendron*, and *Drimys*. (*After Bailey and Thompson.*)

The above characters are grouped as specialized (*i.e.*, advanced in the evolutionary sense) or unspecialized, as follows :—

Unspecialized.	Specialized.
Scalariform vessel pores.	Simple vessel pores.
Fibre tracheids.	Libriform fibres.
Apotracheal parenchyma.	Paratracheal parenchyma.
Diffuse-porous.	Ring-porous.
Unstoried structure.	Storied structure.

Specialized and unspecialized features are widely distributed among angiospermic families and show no relation to specialized or unspecialized floral structure, but truly natural families are usually fairly homogeneous in their type of wood structure.

12. *The Pith.* The comparative anatomy of **pith** is still to be written, though it is evidently a very variable tissue. Many herbaceous plants, notably among the Umbelliferae and Compositae, have hollow stems, due to the failure of the pith to keep pace with the expansion of the outer tissues. The pith thus becomes cracked and riven, or **fistular** as it is called, only a few scanty fragments of tissue remaining to line the cavity. Certain woody plants, of which the Walnut (*Juglans regia*) is the best known, have a discoid pith, due to transverse cleavage, which, consequent upon growth in length of the young shoot, separates the pith into a series of discs, 2 to 3 mm. apart.

The pith often becomes sclerotic, especially at the nodes, and nodal plates of highly thickened cells may remain even when the pith has disappeared in the internodes. The outer zones of the pith are frequently smaller celled, more sclerotic and more persistent than the central portion, forming a conspicuous boundary layer, called in German "Markrande," though an international name has not been adopted.

THE ARBOREAL AND HERBACEOUS HABITS

There has been some controversy on the question whether the arboreal or the herbaceous habit of growth is primitive in Angiosperms. Arguments may be adduced on both sides. In favour of the arboreal habit there is the fact that the earliest known fossil Angiosperms appear to belong almost exclusively to tree families. Further there is the present predominance of woody forms in tropical climates, together with the parallels which can be drawn between woody tropical species and related herbaceous species in temperate climates; the argument being that the herbaceous habit is an adaptation to the severity of winter. On the other side is urged the fact that the youngest stages of tree species are herbaceous, which is an appeal to the theory of recapitulation (see Volume III). Moreover a parallel can be drawn between the great stature of trees with the large mass of their non-living tissue and the gigantism and heavy bone-structure of decadent animal groups of the past, such as the Mesozoic reptiles.

There are undoubtedly many primitive characters in the structure of trees. These have been attributed to the longer life of the tree and the smaller number of generations which such species have passed through in a given time, but nevertheless the balance of evidence is generally held to be in favour of the arboreal theory.

Two interesting anatomical theories have been propounded on the supposed mode of origin of the herbaceous habit from the arboreal, which may be thus briefly summarized :—

1. *Theory of Jeffrey.* Where leaf traces enter the vascular cylinder there is a need for storage for the photosynthetic products of the leaf. This is met firstly by a concentration of medullary rays flanking the traces (aggregate rays). Secondly, these fuse into broad compound rays and the neighbouring woody tissue becomes transformed into storage parenchyma, so that the woody cylinder is broken into separate wedges with broad rays between, through which the leaf traces pass out.
2. *Theory of Sinnott and Bailey.* The herbaceous habit may be attained in two ways, firstly and more simply by the reduction of cambial activity, so that the stem is furnished with a continuous, but thin, ring of wood which soon ceases to expand. Secondly by the reduction of cambial activity in the sectors *between* the leaf traces, the wood there formed being first lessened and finally abolished, leaving broad parenchyma tracts between the separate wedges of wood to which the vascular ring is thus reduced.

Detailed anatomical evidence can be produced for all these processes, and it seems possible that each of them may have been operative in different cases (Fig. 893).

The anatomical features which we have discussed above have more relation to the Dicotyledons than to the Monocotyledons, in which no process of timber building occurs. Some Monocotyledons, however, such as the Palms, form apparently woody trunks by a process which is quite special to them, and which may be called **diffuse thickening.** In the early stages of their development, the apical meristem broadens year by year, with very little growth in length. On this broad meristem the number of leaf primordia increases progressively, with a consequent increase in the number of trace bundles in the stem. The shape of the stem is that of an inverted cone, usually partly buried in the soil. When growth in length begins the stem shoots up into a cylinder, no further growth in girth occurring. No cambium is formed in the bundles, which remain permanently distinct. Each bundle is surrounded or partly surrounded, from an early stage, by a belt of sclerenchyma, and the only alteration of the tissues with age is the increased thickening of the cell walls, which may in time involve the whole of the ground tissue. A very solid stem may thus be formed, even though it contains no mass of wood, and although the parenchyma cells of the ground tissue may remain alive and are often filled with stored starch grains.

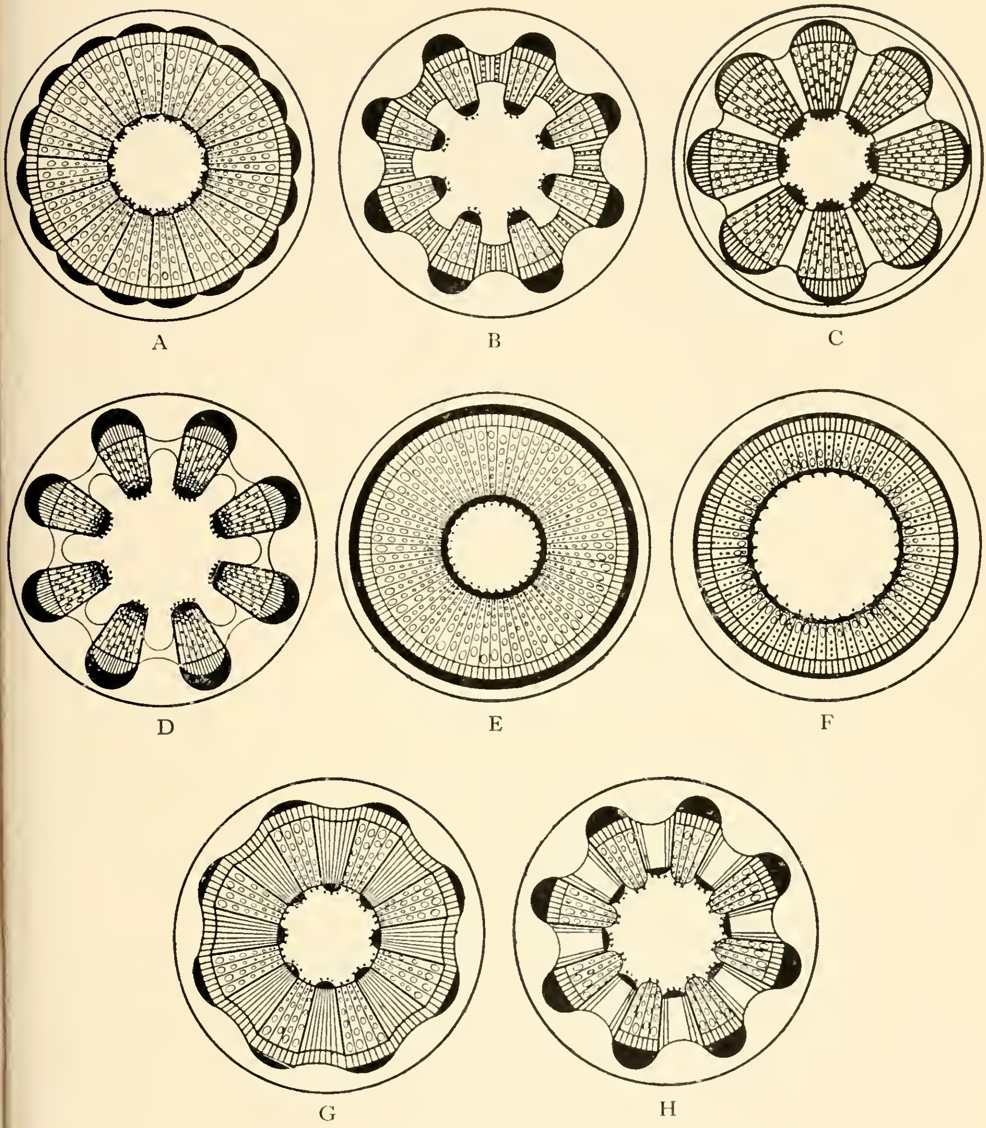


Fig. 893.—Diagrams illustrating the probable origin of the herbaceous type of stem. A, Woody stem with all rays narrow. Crosses indicate protoxylem. Bundles in solid black, next to the pith, become leaf traces. B, Herbaceous stem derived from A by conversion into parenchyma of segments alternating with the leaf traces. C, Woody stem with broad foliar rays. D, Herbaceous stem derived from C by increase in width of broad rays and decrease in their radial extent. E, Woody stem with all rays narrow and continuous protoxylem ring. F, Herbaceous stem derived from E by decrease in cambial activity. G, Woody stem with narrow rays aggregated opposite the protoxylems. H, Herbaceous stem derived from G by conversion into parenchyma of the segments opposite the leaf traces (Jeffrey). (*After Sinnott and Bailey.*)

A concentration of smaller trace bundles and associated sclerenchyma strands at the periphery of the stem forms a mechanically strong rind, which in these stems takes the place of periderm. The inner tissues are relatively unimportant mechanically.

A small group of genera in the Agarales also produce woody stems, notably *Yucca*, *Aloë*, *Dracaena* and *Cordyline*, by a different and peculiar process. We have already mentioned the existence of a bundle cambium in many Monocotyledons, which produces a very limited amount of secondary xylem, though no continuous cambium is formed. In the genera cited above a broad meristematic zone arises in the inner cortex, closely surrounding the central group of primary bundles, that is to say, it occupies the position of a pericycle (Fig. 894). In some species this zone is already differentiated in the apical meristematic region, while in others it appears only towards the base of the main stem, where all the tissues are fully differentiated. It is composed of squarish, thin-walled parenchyma, arranged in radial rows (Fig. 895). It resembles a cambium and is usually so called, but it differs both in origin, structure and behaviour from typical cambia. The radial rows are not the products of division of a single initial cell, but are built up by the successive divisions of three, four or more cortical cells in radial files. The individual cells are not cambiform and do not segregate xylem inwards and phloem outwards, but produce entire, closed, fibro-vascular bundles, within the zone, by the sub-division of single or of grouped meristematic cells. These new bundles arise close together in centrifugal succession, and as they mature the parenchyma between them becomes lignified, so that a remarkably solid band of secondary tissue may be built up in the course of years. Old stems of *Aloë* and some other genera have even been observed to show annual rings of growth.

The Mechanical Properties of Tissues

The sclerenchymatous tissue of plants is regarded as mechanical in function, adding strength to the various organs, and it has been classified as a distinct tissue system, under the name of **stereome.** It is naturally best developed in organs which have comparatively little wood, such as herbaceous and monocotyledonous stems. Besides sclerenchyma the stereome includes also the collenchyma, which is inferior in strength to the sclerenchyma but is more flexible. Schwendener in 1874 published his researches into the mechanical properties of stereome tissues and showed how their distribution fulfilled certain mechanical principles of construction, suitable to the type of strain to be encountered. In stems these are mostly transverse, bending strains, and in roots longitudinal, pulling strains.

For the end to be served the properties of plant fibres are suitable. Thus they have a high modulus or limit of elasticity, and they can suffer considerable elongation without permanent deformation, but beyond this limit, they soon reach their breaking point, further resistance being probably valueless after permanent elongation has occurred, which must inflict irreparable

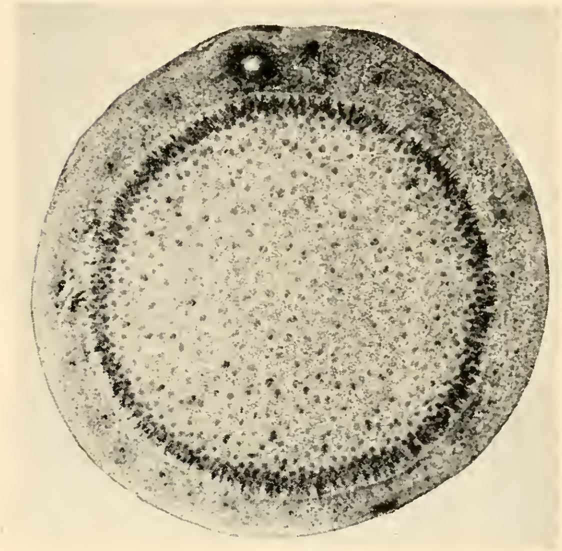


FIG. 894.—*Dracaena sp.* Transverse section of a stem showing scattered primary bundles in the centre surrounded by a compact zone of secondary bundles.

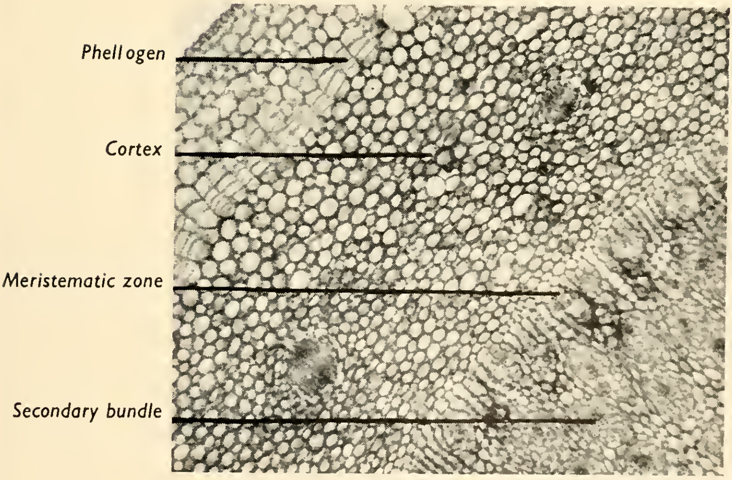


FIG. 895.—*Dracaena sp.* Transverse section of part of a stem showing the meristematic zone with secondary bundles in course of formation.

damage on the neighbouring tissues. A comparison of several plant fibres with metal wires is given below, from Schwendener's figures :—

Plant or Metal.	Modulus in Kilograms per Square Millimetre.	Breaking Strength in Kilograms per Square Millimetre.	Percentage Elongation at the Elastic Limit.
Dracaena indivisa .	17	21·8	1·7
Phormium tenax . .	20	25	1·3
Dasylirion longifolium .	17·8	21·6	1·33
Allium porrum . .	14·7	17·6	3·8
Nolina recurvata .	25	...	1·45
Wrought iron . .	13·1	40·9	0·07
Mild steel . .	24·6	82·0	0·12

Schwendener interpreted the distribution of mechanical tissue, by a comparison with the ironwork of his own day, as representing an arrangement of girders.

In the ordinary I-girder the top and bottom portions are called the "flanges," and the upright middle portion the "web." When such a girder is subjected to a bending strain in the plane of the web it is the two flanges which supply the greatest part of the resistance ; the web is of minor importance and may be made of much lighter material. The flange nearest the side of the applied force is subject to an extension strain, while the other suffers a compression strain. Midway between them is the null-line, where neither strain operates and which therefore provides no part of the resistance. The strain in each portion of the cross-section of the girder is proportional to its distance from the null-line.

The same principles apply to the resistance of a cylindrical column of homogeneous material, and it is obvious that the strength of the column must depend principally on the strength of its outer zones. The centre may indeed be hollow, *i.e.*, tubular, with very little loss of strength.

Schwendener analyzed the mechanical tissues of stems and leaves according to these principles. He classified the structures found in Monocotyledons alone into twenty-eight mechanical types, each with a characteristic girder structure. His girders are nearly all made up of sclerenchymatous flanges, with xylem or collenchyma tissues forming the webs. In some cases the girders are isolated fibro-vascular bundles, in others they are united side by side into tubes, sometimes supported by radial flanges, while in some cases either separate flanges or whole girders form opposing systems across the stem. A good example of such girder construction is shown in Fig. 896.

Engineering practice has advanced since 1874, and in the light of experience in the design of ferro-concrete structures, it is possible to get a fuller idea of the mechanical principles of plant construction. The weakness of Schwendener's theory was that it treated the sclerenchyma as if it was an isolated system and left out of account the softer tissues in which it is embedded. These tissues are, however, to the sclerenchyma what the concrete is to the embedded iron framework. The turgid cells of the ground tissue support the framework of sclerenchyma and take up part of the strain, so that the stress in the mechanical strands is greatly lessened. The similarity between a reinforced concrete column and a monocotyledonous stem in this respect is shown by the comparison of the stress diagrams in Fig. 897, which show that the stresses in the individual sclerenchyma strands are not those typical of girders.

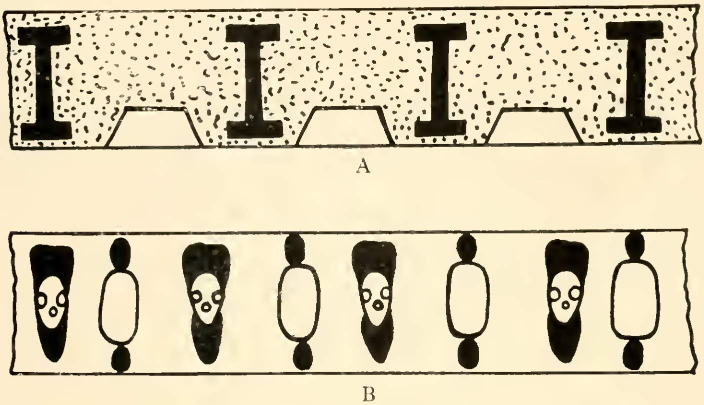


FIG. 896.—Comparison of the section of a reinforced concrete bridge (A) and a transverse section of the leaf of *Phormium tenax* (B). (*After Rasdorsky.*)

The ground tissue has advantages over concrete, in its own inherent flexibility and elasticity, as well as in its perfect adhesion to the sclerenchyma, which permit a considerable degree of bending of the organ without that risk of rupture which would occur in a similar concrete structure.

The close similarity of plan in the natural and the artificial constructions is well illustrated by the comparison in Fig. 898.

In the lamina of a monocotyledonous leaf, especially if flat, the girder model is more closely approached, each vascular bundle with the sclerenchyma above and below it forming one girder.

Roots, which have to withstand only compression and extension strains, have the mechanical tissues, vascular tissues and sclerenchyma combined, forming a single, composite, axile strand, which, like a cable, provides the maximum degree of resistance to extension. This type of arrangement is seen at its best in roots and rhizomes of Monocotyledons. In Dicotyledons there is as a rule only a small amount of sclerenchyma and resistance may be afforded by the xylem alone.

From the foregoing account it will be realized that although lignified tissues have the highest mechanical value, yet the mechanical requirements of the plant's architecture are shared to some degree by all its tissues, and the sclerenchyma does not deserve the name of the " mechanical system " which is often given to it. Balance and resistance to strain are functions which are inherent in the whole structure of a land plant, just as much as are the requirements of photosynthesis or of reproduction.

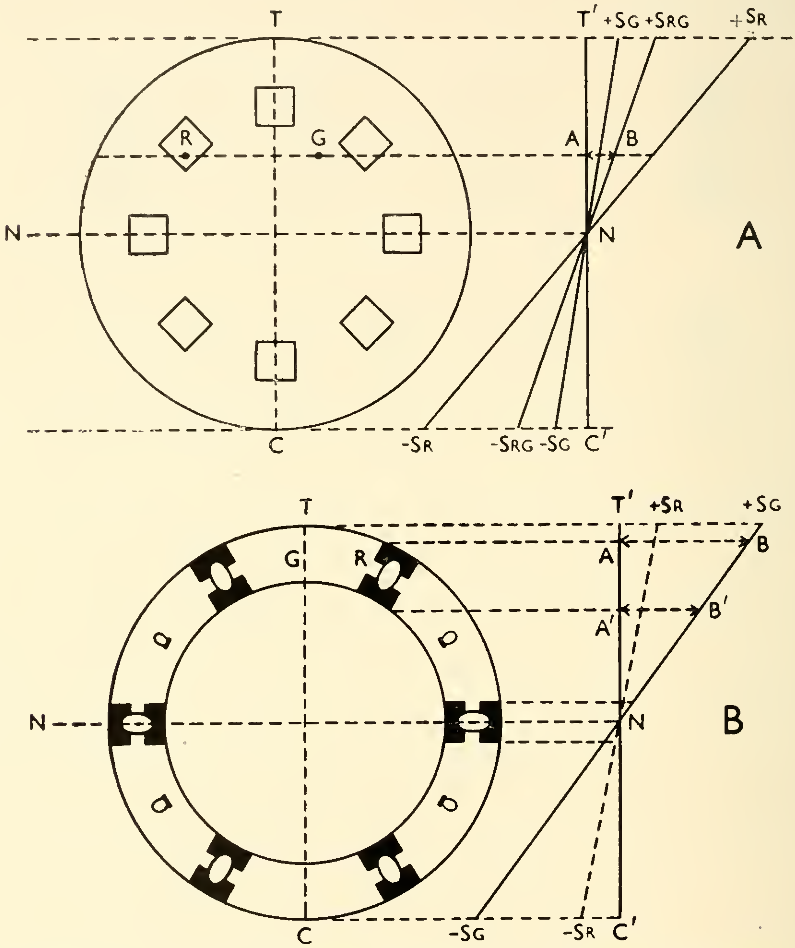


Fig. 897.—A, Theoretical transverse section of a reinforced shaft. The small squares represent the iron rods (R). The concrete mass marked G. The distribution of stresses is represented graphically on the right. TC = the load line. C = compression side. T = tension side. NN = the null line of no load. In the stress diagram SG = stress in ground mass, SR = stress in reinforcement. SRG = stress in combined materials. AB = equal stress at points R and G which are equidistant from the null line.

B, Diagrammatic transverse section of a stem of *Scirpus caespitosus*. The sclerenchyma is coloured black. Symbols as in diagram above. AB = stress (tension) at the outer side of bundle R, and A′B′ = stress (tension) at the inner side of bundle R. Both sides of bundle R are in tension; it does not therefore act as a girder, the only bundles acting as girders in this case are those lying on the line NN, of which one side is in tension and the other side in compression. (*After Rasdorsky.*)

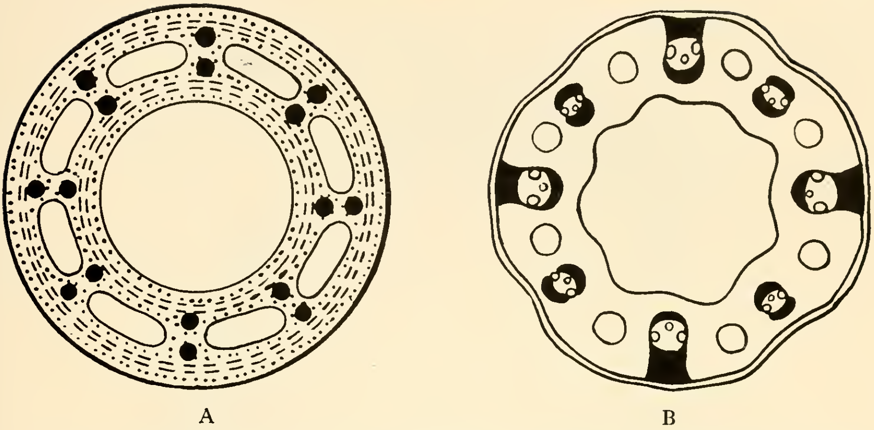


Fig. 898.—Comparison of the section of a reinforced concrete chimney (A) and a transverse section of the stem of *Trichophorum germanicum* (B). The sclerenchyma strands marked in black correspond to the iron rods; the ground tissue corresponds to the concrete. (*After Rasdorsky.*)

Anomalous Structures

So great is the number of Angiosperms and so infinitely various their structure, that it is difficult to say what should be considered anomalous, where the normal itself can scarcely be defined. We can only select for mention a few examples of peculiarities which are non-environmental, that is to say, are not directly related to the external conditions.

1. *Phloem and Xylem Strands.* Separate strands of phloem only, in addition to the normal collateral bundles, are not uncommon in flower and fruit stalks, presumably in connection with the need for a large inflow of carbohydrates to the fruit during seed ripening. Pure xylem strands are less common, but they occur in the tubers of the Paeony.

2. *Medullary Bundles.* Accessory bundles, in the pith, are found in many Dicotyledons, and are characteristic of a few families, such as the Piperaceae (Fig. 899), members of which possess from one to four rings of such bundles interior to the normal ring, which alone undergoes secondary thickening. These bundles belong to the leaf traces. They descend through one internode in the normal ring and then curve inwards and pass through another internode in the pith. The two rings of bundles which are usually formed in Cucurbitaceae (Fig. 900) are likewise all connected to the leaf traces. The numerous medullary bundles in *Begonia* do not appear to become leaf traces but they anastomose freely with those that do and so form part of the trace system.

Some dispute exists about the presence of truly " cauline " bundles in the stems of Angiosperms. The medullary bundles in *Amaranthus*, for example, like those in *Begonia*, are cauline in the sense that they are not themselves actual leaf traces, but they branch from and join with leaf traces, so that they are physiologically part of the leaf trace system. Whether they arise in the meristem as purely stem structures without relation to the leaf rudiments has not been settled.

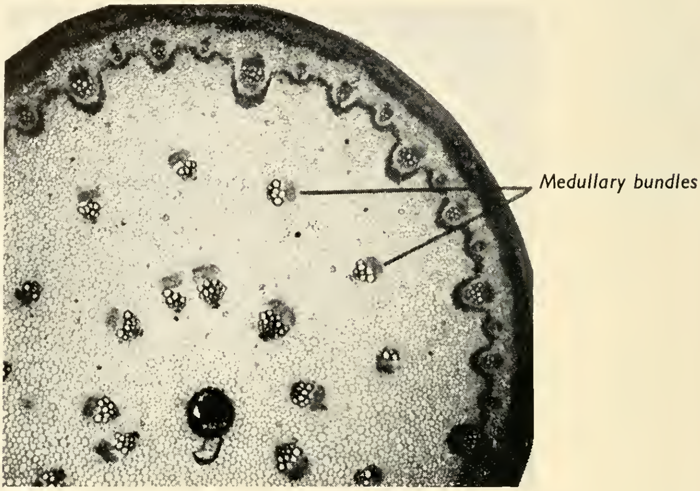


FIG. 899.—*Piper clusii.* Transverse section of stem showing accessory bundles in the medulla.

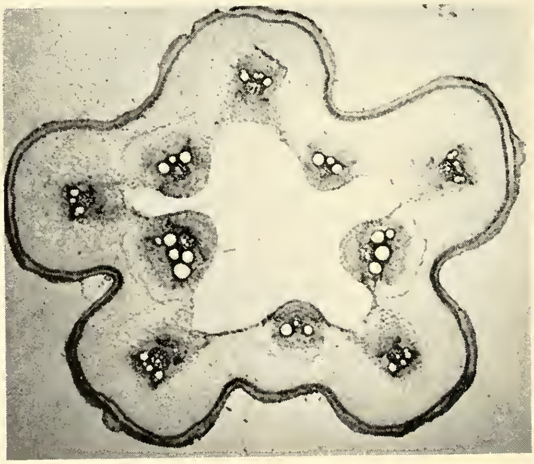


FIG. 900.—*Cucurbita pepo.* Transverse section of stem showing two rings of vascular bundles. The central cavity represents the space previously occupied by the pith.

3. *Scattered Bundles in Dicotyledons.* These cases are only separated from the above by the fact that there is no normal ring of bundles, but all are irregularly scattered, or arranged in two or three irregular zones. Such cases are known chiefly in Ranunculaceae (Fig. 901) (*e.g., Thalictrum*) and Berberidaceae (*e.g., Podophyllum*) and also in *Papaver.* They seem to be associated with leaves with wide bases and numerous trace bundles.

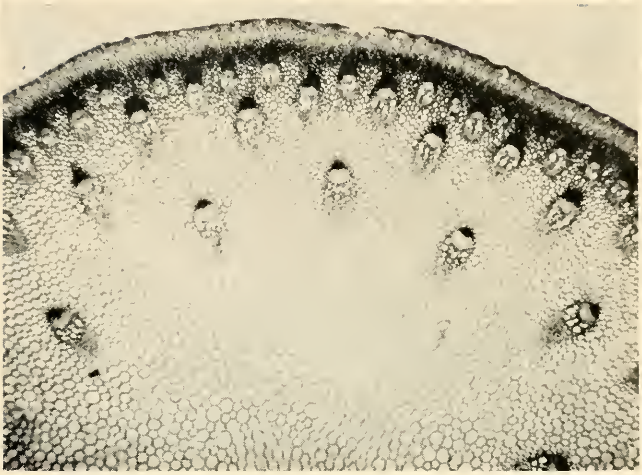


FIG. 901.—*Anemone japonica.* Transverse section of stem showing the monocotyledonous arrangement of vascular bundles in the stem of a Dicotyledon.

4. *Ring Arrangement in Monocotyledons.* A well-known case is that of *Tamus communis* (Fig. 902), in whose stem internodes the bundles are all peripheral, forming an irregular ring around a large pith. It is noteworthy that *Tamus* has petiolate, net-veined leaves like those of a Dicotyledon.

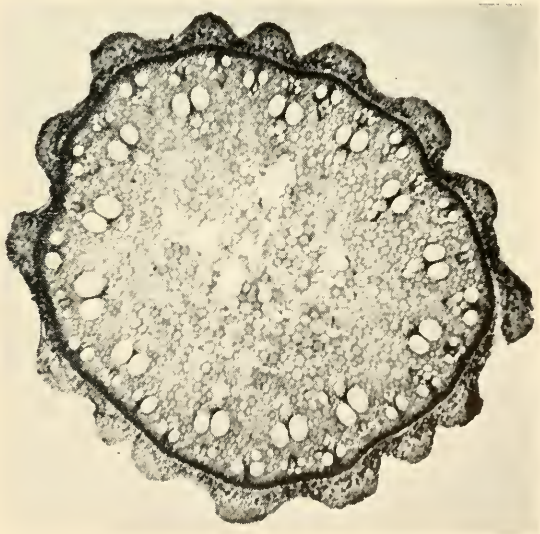


FIG. 902.—*Tamus communis.* Transverse section of the aerial stem showing ring arrangement of bundles in a Monocotyledon.

A bundle ring is also typical of Monocotyledons with tubular stems, such as the grasses, where it is a necessary consequence of the hollow internodes.

5. *Cortical Bundles.* These are leaf trace bundles, usually lateral ones, which do not enter the ring but pursue an independent course through the cortex. They may either enter the ring at a lower node, as in *Begonia*, or they may unite with the cortical bundles of the next internode below, thus forming an independent system connected to the ring only by nodal anastomoses, as in *Calycanthus* (Fig. 903).

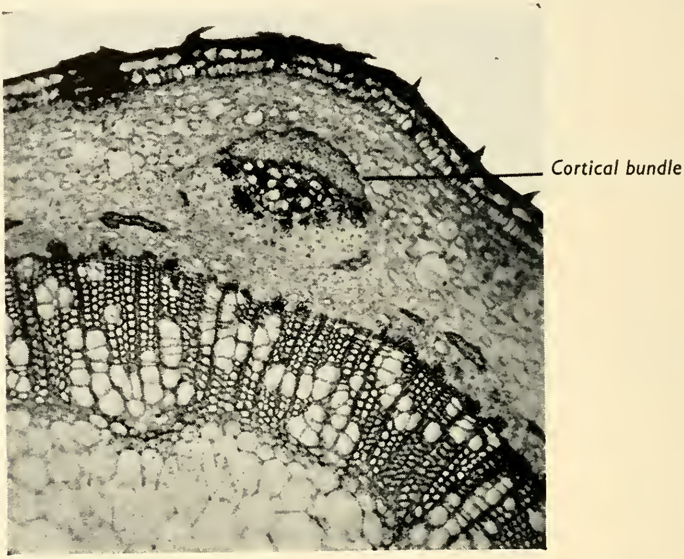


Fig. 903.—*Calycanthus floridus.* Transverse section of stem showing one of the cortical bundles.

6. "*Polystely.*" This term has been applied to the condition found in some dicotyledonous types, *i.e.*, *Gunnera*, *Primula auricula* and some related species of *Primula*, and in the Nymphaeaceae. The stem contains an irregular network of connected bundles to which the leaf traces are joined. There is no secondary thickening, the number of bundles increasing as the stems thicken with age, as in Monocotyledons. The network is, however, much more complex than in most of the latter group, though a similar structure is characteristic of the Araceae. Each bundle has its own endodermis and should therefore be a meristele, and the whole network has been called an Atactostele, but it is probable that these meristeles are only concentric amphiphloic bundles (Fig. 904). The suggestion has been made that this peculiar condition has arisen secondarily from the reduced, central stele characteristic of many water plants. When the stems subsequently increased in size, by adoption of the land habit or otherwise, there was a need for more vascular tissue. The capacity for secondary thickening having been lost it is supposed that the need could only be met by the branching of the single stele.

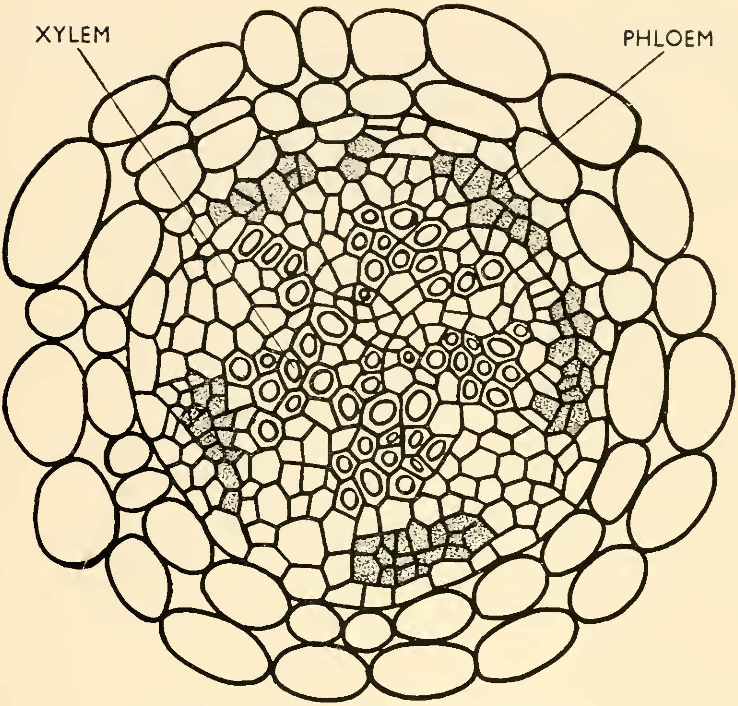


FIG. 904.—*Primula auricula.* Single meristele which is probably a reduced amphiphloic bundle. (*After Bouygues.*)

7. *Inverted Bundles.* In certain cases, of which *Rumex crispus* and *Rheum officinale* are examples, phloem strands appear on the medullary side of the primary bundles, and on the outer edge of each phloem strand arises a secondary cambium, which cuts off xylem elements *outwards*, the inner bundles thus appearing like primary bundles, but with inverse orientation of tissues (Fig. 905). A second inverted ring may even be formed inside the first. Such inverted orientation also occurs in some forms of anomalous secondary thickening, especially in climbers.

8. *Repeated Concentric Rings of Bundles.* Examples of this structure have already been cited in the roots of Chenopodiaceae such as *Beta*, and in the stem of *Gnetum gnemon.* It is not uncommon in the secondarily thickened stems of woody climbers, as we shall see in Volume IV, but it also occurs in thickened stems where it is not associated with a special growth habit, *e.g.*, *Phytolacca dioica.* Here a secondary growth zone of tangentially dividing cells appears at the outer edge of the phloem, *i.e.*, in the pericycle of the first, normal ring of bundles. This growth zone expands outwards into a zone of parenchyma, at the outer edge of which a true secondary cambium is formed, from which a second ring of vascular bundles is differentiated. This in its turn is replaced by a third zone of bundles formed in the same way, and so on till six or seven concentric bundle rings have been formed. Cambial growth in each ring ceases when the next ring has been formed.

A similar arrangement may be reached in quite a different way, as in *Amaranthus*, where the pericyclic secondary cambium remains permanently active, and forms successive zones of ground tissue and of collateral vascular bundles, all from its inner side, while on the outer side it forms only a little phloem or nothing at all.

9. *Phloem Islands.* This type of structure, also associated with many climbers, is found in certain families of non-climbers, notably the Chenopodiaceae. The mature stem shows a vascular zone of normally arranged xylem and phloem, but in the secondary xylem are a number of isolated islands of phloem. These are formed by the enclosure of portions of the normal phloem by short arcs of secondary cambium formed externally in the pericycle. This cambium cuts off xylem on its inner side, that is to say, outside the enclosed portion of phloem, which is thus bridged in by xylem tissue (Fig. 906).

The foregoing examples of anomalous structures are selected because they have no relationship to any peculiarity in the growth habit or environment of the plants, but are rather such as are characteristic of particular systematic groups in which they are hereditary. They are thus " phyad " structures, in the sense of Grisebach, rather than " ecads." The latter class of anomalies, which are ecologically conditioned, will be dealt with in Volume IV.

Morphological Modifications of the Stem

The type of stem which may be regarded as normal is that which is prevalent among Dicotyledons, namely an elongated, radially symmetrical structure, bearing foliage leaves at nodes placed at graded intervals. Although this corresponds to the general idea of a typical stem, it must be remembered that throughout the Monocotyledons the stem is usually much contracted and often subterranean, and that among the Dicotyledons there are large groups within which the definition scarcely applies. We began this chapter by emphasizing the protean nature of stems, and it needs only a superficial acquaintance with plants to realize the truth of that remark. Even a wide knowledge, if derived only from temperate floras, would give but a limited idea of the morphological possibilities of the stem, and it would be rash indeed to attempt to lay down general laws of stem structure or to formulate a definition of a stem intended to be all-embracing.

There is a considerable amount of " division of labour " among the shoots of perennial plants, orthotropic shoots being often specialized for climbing or for flower production, and plagiotropic shoots for various functions, including especially food or water storage and the vegetative propagation of the plant. These modifications are sometimes related to special environments or growth habits, and such will be dealt with in Volume IV. In the majority of cases, however, they are not related to special conditions, but are the result of, so to speak, inborn habit. How far such habitual modifications are fixed, *i.e.*, genetical, and how far they are changeable by external conditions, varies greatly in different cases. Few characters in plants are

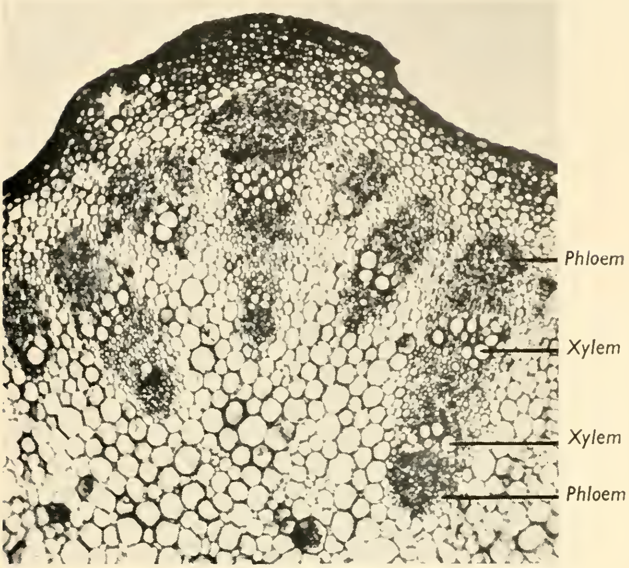


FIG. 905.—*Rumex crispus.* Transverse section of stem showing vascular bundles with inverted orientation attached to the inner side of the large vascular bundles of the normal ring.

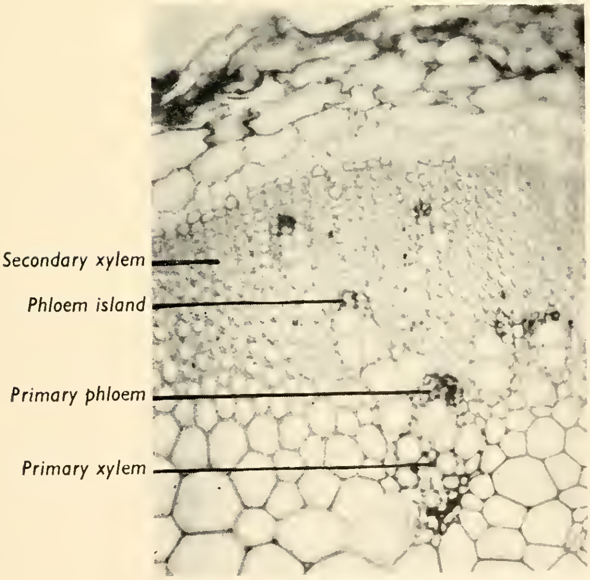


FIG. 906.—*Suaeda fruticosa.* Transverse section of stem with secondary thickening showing phloem islands included in the zone of secondary xylem.

completely resistent to changes in the environment, and there is little in the vegetative kingdom which accords with the doctrine expressed by the German word "anlage," which involves the idea of a predetermined development, supposed to be inherent in a given organ rudiment.

We shall select certain outstanding examples of habitual modifications, without regard to the question of their fixity or mutability. The larger works of systematic Botany will provide the student with countless other instances.

Modifications of the Aerial Shoot

1. *Cladodes and Phylloclades.* The term **cladode** is applied to a branch of a single internode which is flattened to simulate a leaf, and the term **phylloclade** to entire shoots similarly flattened and leaf-like. There are considerably more cases in the latter category, and it is not always easy to discriminate the one type from the other, with the result that many botanists treat them as synonymous.

The biological principle is the same in both, namely the replacement of reduced leaves, which are no longer functional for photosynthesis, by flat branches, containing chlorophyllous tissue, which function physiologically as leaves. The benefit to the plant of such a procedure is indeed puzzling, inasmuch as the cladodes are never as efficient photosynthetically as are true leaves. Perhaps we have here an example of the supposed "Law of Irreversibility" in evolution, which maintains that a structure once lost cannot be regained but can only be substituted by the modification of other existing structures. As such a substitution necessarily involves the production of new characters in the structures concerned, it is difficult to understand what should prevent the redevelopment of the lost character as the simplest response to the demand of necessity. But to these questions there are no adequate answers.

A good example of a simple cladode is that of *Ruscus aculeatus* (Butcher's Broom) (Fig. 907) and of some related plants such as *Semele* and *Danaë*. The cladodes are short, ovate, spiny-pointed and with parallel veins. They are deep green in colour and arise in the axils of minute scale leaves, which soon drop off. In the young shoot of *Ruscus* these leaves are much bigger and partly green ; the cladode habit is only fully established in mature shoots. Each cladode bears, half-way up and in the median line, a scale-like bract, from the axil of which arises in summer a group of flowers.

There has been much dispute about the morphological nature of this structure. The classical view is that the whole structure is a branch of limited growth bearing one node from which arise the flowers, subtended by the small bract. Opposed to this is the view that only the lower half is axial in nature and that at its apex (the flower bearing "node") are two opposed bracts, one small and one large, the latter forming the upper half of the cladode, with its margins decurrent along the lower, axial portion. This latter view, though it seems far-fetched is, in fact, supported by the vascular structure, which is axial only in the lower and leaf-like in the upper half, and also by the presence of opposed bracts in the related genus *Danaë*, where the inflorescence is free from the cladode. A third theory interprets the whole cladode as a modified leaf, borne on an axillary shoot, to which it is united along its lower half.

FIG. 907.—*Ruscus aculeatus.* Shoot with cladodes bearing flower buds.

The common Asparagus (*A. officinalis*) has cladodes which appear from the axil of each scale leaf as two little bundles of green needles. Comparison of the placing of these, relative to the scale leaf, with the arrangement of the flowers at flowering nodes, makes it very probable that they represent sterilized flower stalks arranged in two cymes. They do, in fact, occasionally bear abortive flower buds at their ends (Fig. 908).

The median axillary shoot, present at the flowering nodes, is suppressed at the vegetative nodes, but in the allied genus *Myrsiphyllum* (Climbing Asparagus) it is present and is developed into a leaf-like cladode, instead of the needles of the common Asparagus, which in this case are suppressed.

As true phylloclades in our present sense, we may cite several cases in which the whole of a shoot or indeed all the shoots of the plant are flattened and leaf-like. Perhaps the best known is the Cactus called *Opuntia* (Prickly

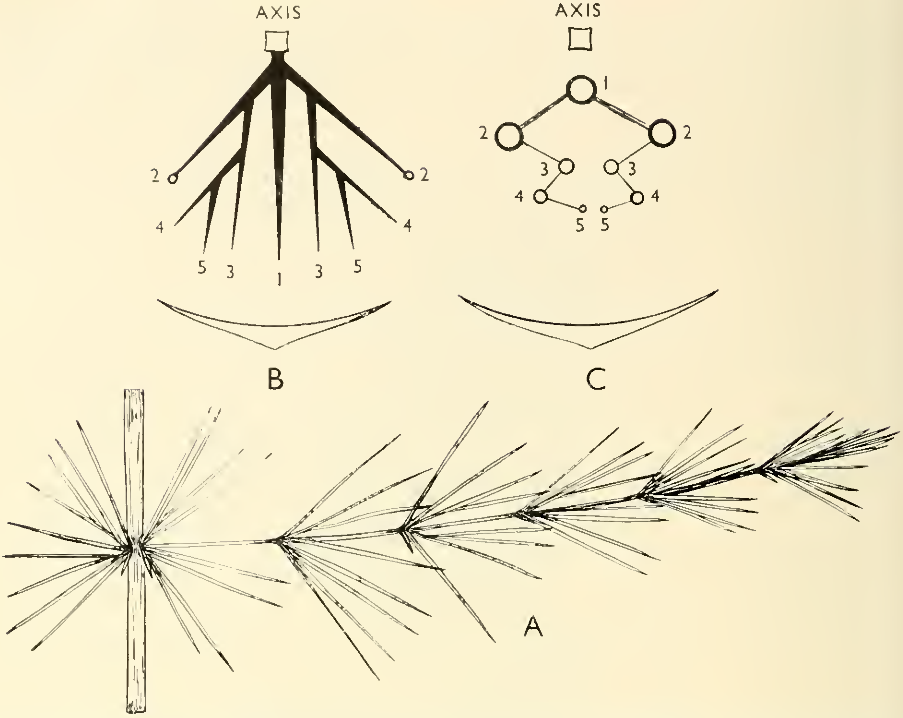


Fig. 908.—*Asparagus officinalis.* A, Shoot showing the arrangement of the needle-like cladodes in reduced axillary cymes. B and C, Diagrams illustrating the order of development of the cladodes in a cyme. (B and C *after Eichler.*)

Pear), the shoots of which form large discoid segments (Fig. 909). The apex is, however, radially symmetrical, and in some species all the shoots are globose or cylindrical. Some other species of the Cacti are also flattened, notably among those which form the genus *Epiphyllum*, frequently grown for the sake of its large scarlet flowers. None of these Cacti has any true leaves. This is probably connected with their desert habitat, but the flattened shoots are a peculiarity of these genera, not necessarily related to the environment.

In the genus *Muehlenbeckia* (Polygonaceae) and *Carmichaelia* (Papilionaceae) (Fig. 910), from the southern hemisphere, the shoots may form jointed green ribbons, but temporary leaves are produced at the nodes in spring.

Certain species of *Phyllanthus* (Euphorbiaceae) show an interesting example of what we may call pseudo-phylloclades. The main shoots bear only scale leaves from whose axils arise side shoots of limited growth, which are pinnately branched and bear small true leaves in two lateral rows. The whole appearance of these shoots is exactly that of the pinnately compound leaves of such leguminous plants as *Mimosa*. In other species of *Phyllanthus* the lateral shoots are true phylloclades.

2. *Thorns.* True stem thorns are distinguished from prickles by their branch nature (Root thorns, see p. 824).

Prickles are modified trichomes (see p. 869), and spines are usually

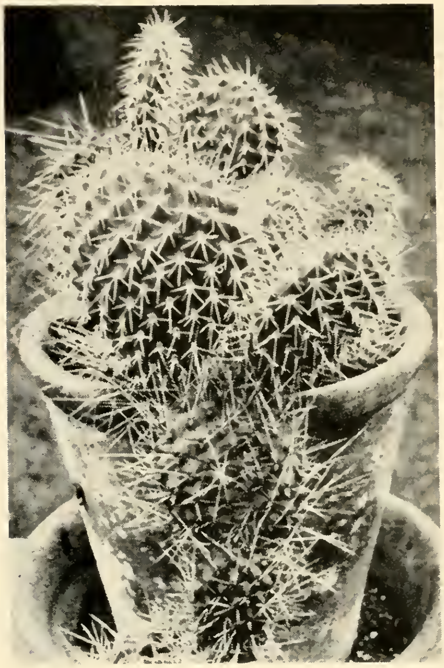


Fig. 909.—*Opuntia polyacantha.* Plant showing discoid stem segments.

Fig. 910.—*Carmichaelia australis.* Portion of a flattened shoot.

FIG. 911.—*Hippophaë rhamnoides.* Leafy shoot with thorn branches bearing leaves and secondary branches.

modified leaves or stipules, but thorns arise from leaf-axils and often bear leaves or flowers as evidence of their branch nature. The thorns of *Hippophaë* (Fig. 911) and *Crataegus* (Fig. 912) are examples. They commence in spring as axillary shoots with normal leaves and with an apical bud, and if the shoot which bears them is cut early and placed in water they will continue to grow as normal branches. Left to themselves, however, the apex soon stops growth and hardens into a woody point, from which the undeveloped leaves fall away, leaving it naked. The lower leaves in large thorns may persist, and from their axils may develop secondary thorn branches.

FIG. 912.—*Crataegus oxyacanthoides.* Leafy shoot with thorn branches with leaves.

In *Ulex* (Gorse) (Fig. 913) the main shoots are thickly set with compound

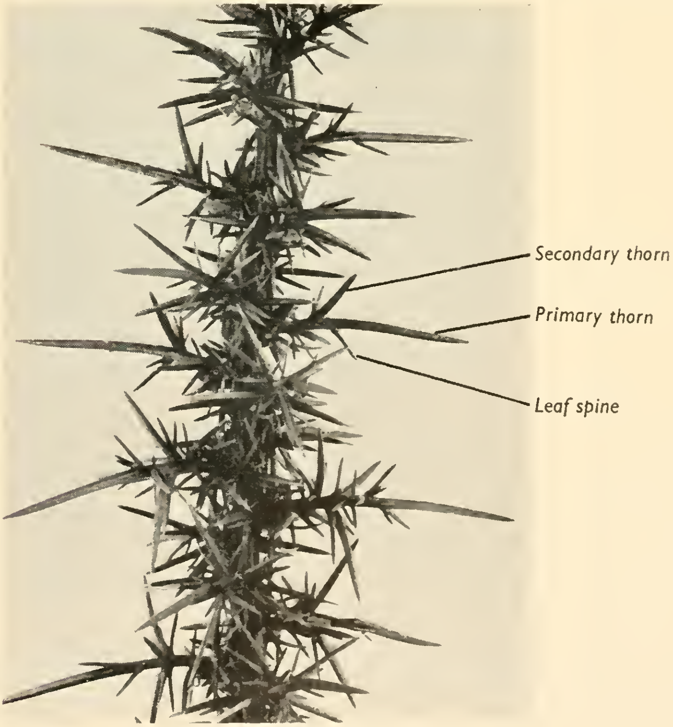


FIG. 913.—*Ulex europaeus.* Shoot bearing compound thorn branches beset with spiny scale leaves.

thorn branches, but in this case the leaves are also reduced to spines and the function of photosynthesis devolves on the branches including the thorns, which are all green. Gorse seedlings raised in a damp atmosphere do not develops thorn or spines, but produce leafy side shoots of reduced growth. A similar change has occurred in the Apple (*Pyrus malus*) which is thorny in the wild state, but not in cultivation, where the thorns are represented by fruiting spurs.

The above examples are all straight thorns, but thorns may also be curved in the form of a hook, as in the South African tree, *Acacia detinens*, from which the unwary may find it almost impossible to escape.

FIG. 914.—*Colletia cruciata.* Flowering shoot showing decussately arranged thorn-cladodes.

Intermediate structures between thorns and cladodes are known. Such for example, are the remarkable flattened branches of *Colletia cruciata* (Rhamnaceae) (Fig. 914), which are unlike other cladodes in being flattened in the vertical direction. They, and the secondary cladodes which grow from them, end in thorn-like points.

3. *Winged Stems.* These provide another example of the stem taking over the photosynthetic functions and something of the structure of leaves. The wings may be mere ridges, as in the Broom (*Cytisus*) or narrow frills as in *Scrophularia alata*, but they are often so developed that they are many times

broader than the stem itself. In many cases the wings are clearly downward prolongations of the leaves or stipules, but in a few cases, notably in *Genista sagittalis* (Fig. 915), they are due to the expansion of the stem tissues. Such cases are distinguishable from phylloclades by the existence of a normally organized stem, to which the expansions are attached (Fig. 916).

FIG. 915.—*Genista sagittalis.* Flowering shoot showing winged stems.

4. *Runners.* These are plagiotropic stems which grow on the surface of the soil, often for considerable distances (Fig. 917). They are a potent means of vegetative propagation (see Volume IV), and they form a natural transition to rhizomes (see p. 933) with which they may sometimes be interchanged, as in *Phragmites.* Normally the Reed produces rhizomes below the surface of the mud on which it grows, but if the ground dries up runners are

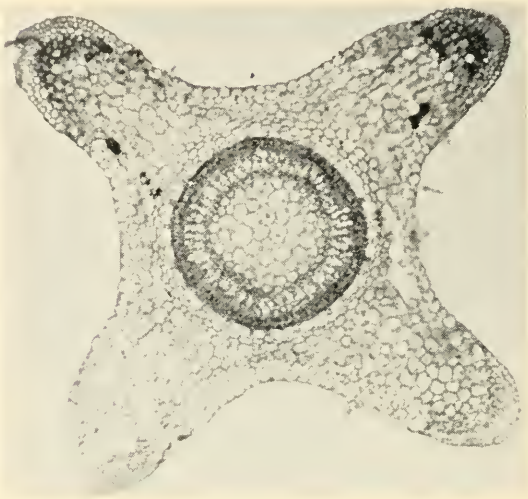


FIG. 916.—*Rubia peregrina.* Transverse section of stem showing stem wings formed as extensions of the stem cortex.

formed above ground, which spread more rapidly than the rhizomes and may be up to 10 metres long.

One of the best-known cases is that of the Strawberry (*Fragaria vesca*), which spreads by runners with extreme rapidity. The runners come from the axils of the leaves on the flowering plant. They bear only reduced leaves, each consisting of a pair of stipules with a small bristle between them. The runner ends at the second node, with a rosette of normal leaves. From the axil of a reduced leaf at the base of this rosette a new runner emerges, and so on. The whole runner is therefore sympodial. Each rosette eventually

FIG. 917.—*Ranunculus repens.* Plant with a runner bearing adventitious roots at two nodes.

produces adventitious roots and becomes independent, for the internodes die off in winter.

Runners are commonest in herbaceous plants, but some shrubs also produce them, such as *Lonicera japonica* and *Rhus toxicodendron* (Poison Ivy).

Modifications of Underground Shoots

1. *Rhizomes.* These are plagiotropic underground stems of the most varied kind. They are found in a vast number of plants. In many species they are thin, tough and rapid in growth, as for example, in *Ammophila arenaria*, *Carex arenaria* (Fig. 918), *Convolvulus arvensis* and *Agropyron repens.* Others have relatively fleshy, though rapidly growing, rhizomes, as *Tussilago farfara*, *Convallaria majalis* (Fig. 919), *Mercurialis perennis*, *Aegopodium podagraria* and *Mentha spp.* A third group of rhizomes are fleshy and stumpy and serve more for storage than for spreading; such are the rhizomes of *Iris germanica*, *Polygonatum multiflorum* (Fig. 920) and *Symphytum tuberosum.* Of this latter class a number are dorsiventral, producing leaves on their upper sides and roots only on their lower sides, besides being often flattened in section. In *Nuphar lutea* and *Nymphaea alba* the dorsiventrality only appears in old rhizomes and is conditioned by light, as they grow on the bottom of ponds. If they are buried in the mud they grow out into radial shoots which turn upwards until they reach the light, when dorsiventral growth is resumed.

FIG. 918.—*Carex arenaria.* Apical portion of a rhizome bearing scale leaves and adventitious roots. Axillary branches grow upwards from the nodes and bear the foliage leaves.

FIG. 919.—*Convallaria majalis.* Portion of a rhizome showing sympodial growth and two terminal leafy buds.

Many rhizomes display an extraordinary capacity for regulating the depth at which they grow. For example, if the dorsiventral rhizome of *Polygonatum multiflorum* (Solomon's Seal) is planted too deep, the growth of new branches is directed upwards until a suitable depth is reached. If it is planted too near the surface the reverse takes place. The physiology of this peculiar response is unknown, but it has been suggested that it is due to the effect of light penetrating the soil. This would imply that the level of growth is a balance of negative phototropism against negative geotropism.

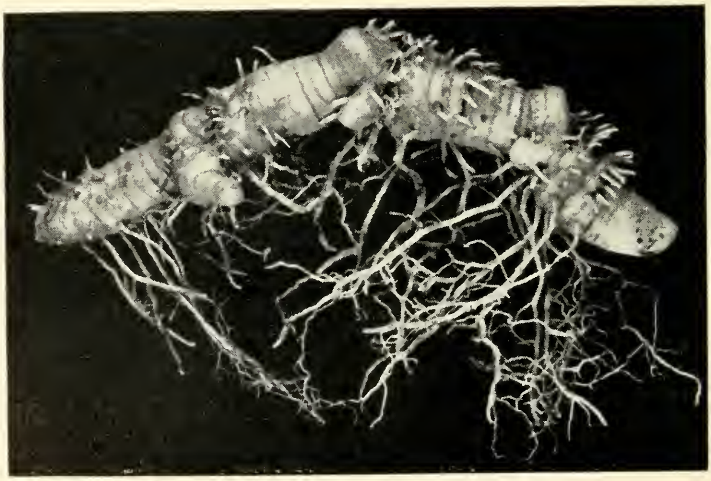


FIG. 920.—*Polygonatum multiflorum.* Portion of the storage rhizome bearing adventitious roots and showing sympodial growth. The large apical bud on the right will develop into an aerial stem.

The apex of a rhizome is always eventually transformed into an upright shoot, which becomes aerial. As this apex has to make its way through the soil it requires protection, which is afforded in one of two ways; either by smooth, hard and pointed scales which provide a boring point, as in *Ammophila*, or by the folding back of the apex into a crook, of which the curved portion is the part which actually penetrates the soil, as in *Mercurialis perennis*. These crooks persist until the apex grows up into the light, after which they unfold. If they are covered from the light they do not unfold, even after they have emerged from the soil.

Rhizomes are nearly always branched sympodially, owing to the orthotropic development of the apex. Lateral branches spread out plagiotropically in the same horizontal plane as the original rhizome, no matter from which side of it they arise. The plagiotropic growth of rhizomes is not, however, invariable. Apart from the exceptional cases of upwardly directed shoots formed as a regulatory measure in rhizomes too deeply buried, there are some instances of the reverse, namely of direct downward growth of a rhizome. These are chiefly in *Yucca*, *Cordyline* and *Dracaena*, shrubby members of the Agavaceae. The downwardly directed rhizome normally functions as a storage organ pure and simple, but if flowering or any accident terminates the growth of the aerial shoot, branches spring from near the base of the rhizome, which become new aerial shoots. The apex of the rhizome does not itself develop thus and will only grow into an aerial shoot if it is turned upside down.


FIG. 921. *Neottia nidus-avis.*—Flowering plant showing the densely branched underground rhizome system.

Although most rhizomes are well provided with adventitious roots, there are a few cases in the Orchids, *e.g.*, *Neottia* (Fig. 921) where no roots occur and the closely branched rhizome system itself functions as an absorbing organ (*cf. Psilotum*, Fig. 619).

Most rhizomes are perennial structures, but many examples occur among herbaceous plants (*e.g.*, *Aster*) in which a crop of short rhizomes is formed round the base of each aerial shoot. They grow only for one season and are next season replaced by a fresh crop, springing from each new shoot, while the old rhizomes rot away. Such plants occupy a limited area of ground with extreme density.

The term stolon is often to be found in older books, applied indiscriminately to various kinds of plagiotropic stems which root adventitiously. It is most generally used for comparatively short, above-ground shoots which are shorter than typical runners. As it has no precise significance it had better perhaps be dropped. The same is true of the term sobole.

2. *Droppers*, sometimes called Rhizomorphic Droppers. These are a special kind of rhizomatous branch, produced from young bulbs (see below) of Tulip, etc. An axillary growing point is covered in by the inrolling over it of a leaf initial, so that it lies inside a hollow hood comparable to a coleoptile. The base of the leaf and the stem immediately below the growing point then elongate greatly, carrying the protected apex outwards and downwards from the parent bulb, the base of the rolled leaf acting as a boring point, until a suitable depth is reached, at which the enclosed growing point may develop into a new bulb (Fig. 922).

FIG. 922.—*Tulipa vitellina.* Garden hybrid. Bulb bearing a dropper branch.

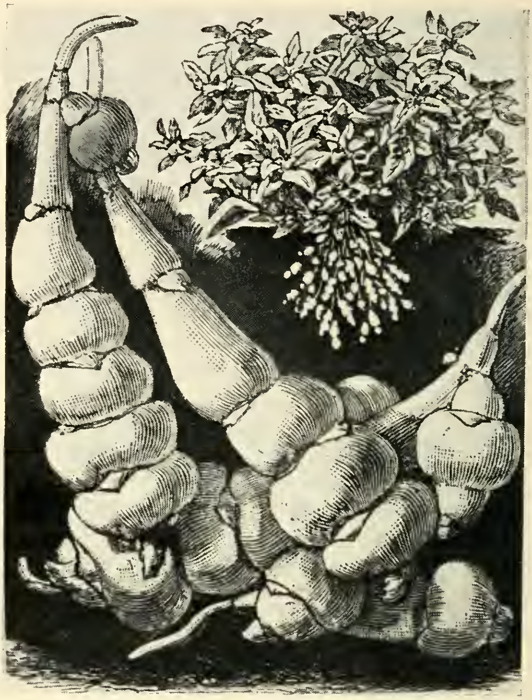


FIG. 923.—*Stachys tuberifera.* Tuberous rhizome. (*From Vilmorin, " Les Plantes Comestibles."*)

3. *Tubers.* These are solid, thickened stems or branches serving for storage and also, if detached, for vegetative propagation. They may be formed on rhizomes, on axillary branches or on main stems, either below or above ground. Rhizome tubers are only distinguishable as such when formed on comparatively slender rhizomes, such as those of *Circaea*, since swollen rhizomes such as those of *Iris germanica* may be regarded as tuberous throughout. In *Circaea lutetiana* and in *Cyperus esculentus* the tubers are terminal on rhizome branches. They contain the terminal bud, protected by scale

leaves, and become centres of new growth when the rhizome connecting them to the parent plant has perished by decay. Those of *Cyperus esculentus*, *Stachys tuberifera* (Fig. 923) and of *Sagittaria sagittifolia* are edible.

Branch tubers may be typified by the Potato. The tuber-bearing branches come from the lowest axils of the aerial stem, even, in seedlings, from the cotyledonary axils. These branches are plagiotropic or weakly geotropic, and if formed above ground they bury themselves and swell out at their apices to form the massive tubers, which bear temporary scale-leaves with buds in their axils called " eyes." The tuber has a corky periderm and may remain dormant for some time. When it germinates, orthotropic shoots are formed from the axillary buds, which become new aerial stems. Even a single detached bud will grow and form a new plant. In some conditions axillary buds near the top of the leafy shoots may be transformed into sessile tubers (Fig. 924). Placing the plant in the dark under a box will often stimulate this abnormal tuber formation. The tubers of the Jerusalem Artichoke (*Helianthus tuberosus*) (Fig. 925) are formed like those of the Potato, but they are borne on shorter branches, are often themselves branched and have persistent, fleshy scale leaves. They contain inulin instead of starch. Similar but more slender tubers are formed by the perennial Sunflower (*Helianthus rigidus*).

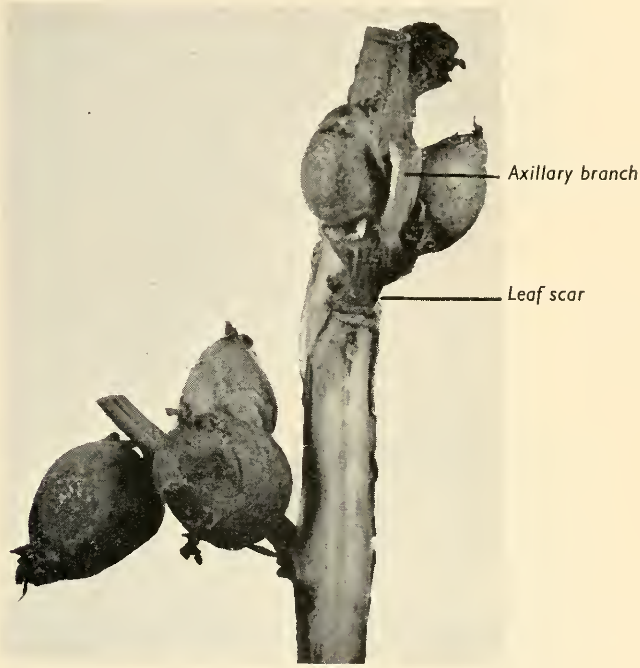


FIG. 924.—*Solanum tuberosum.* Portion of an aerial shoot bearing axillary tubers.

FIG. 925.—*Helianthus tuberosus.* Tuber showing nodal ridges and bud developing into an aerial shoot.

Tubers on the main stems are formed, for example, in a climbing member of the Asclepiadaceae (*Ceropegia woodii*), which is often grown in greenhouses (Fig. 926). The tubers are local thickenings of the nodes, including the bases of the pair of opposite leaves borne at the node, and their axillary buds. They are generally not detached, but form adventitious roots ***in situ***, which attach them to the support (bark, etc.) on which the plant is climbing and so become new centres of growth.

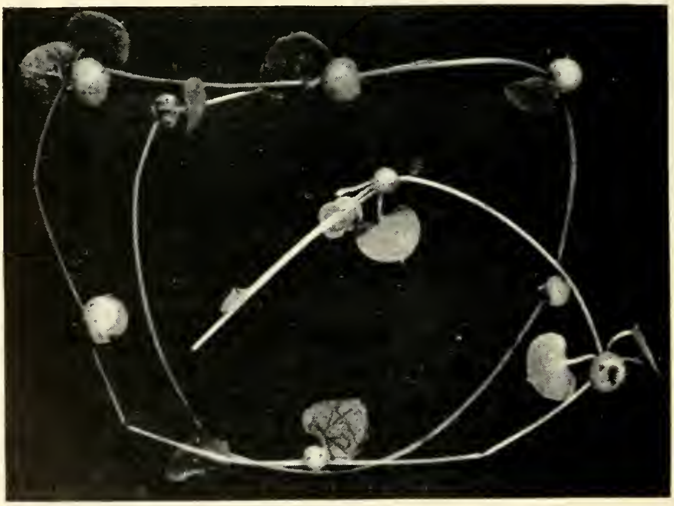


FIG. 926.—*Ceropegia woodii.* Trailing shoot showing tubers formed as swellings at the nodes.

Many members of the Dioscoreaceae form stem tubers. In *Tamus communis* (Black Bryony) the first internode above the cotyledons thickens to form a perennial tuber, which may reach a very large size and may branch. From this tuber the leafy shoots are annually renewed. Another well-known example is *Testudinaria elephantipes*, a South African desert plant (Fig. 927), in which the base of the stem forms a large tuber, as much as 30 cm. across, which stands partly above ground. It is covered by a very thick, irregular periderm which gives it the name of Elephant's Foot. As in *Tamus*, delicate or trailing shoots are produced from the tuber each spring and disappear in the dry season.

Fig. 927.—*Testudinaria elephantipes.* A large woody tuber from which the annual foliage shoots arise.

4. *Corms.* The corm is simply a special form of underground tuber, consisting of a much contracted, swollen, main stem, whose principal axis is vertical. On top it bears an apical bud, from which summer shoots with leaves and flowers are produced, and it bears an annual crop of adventitious roots, usually from the lower end (Fig. 928). Good examples are provided by *Crocus* and *Gladiolus*. Here the corm is considerably flattened, its length being shorter than its diameter. It is covered by a tunic made up of the fibrous remains of leaf bases, which arise from nodes that form a series of ridges around the corm. At the nodes there are occasional buds, axillary to

the scales, from which side shoots and new corms may arise. In *Tritonia* these buds produce rhizomes, which copiously propagate the plant, forming new aerial shoots with new corms at their bases. When flowering is over the leaves of *Crocus* remain active for some time, and the material they assimilate is stored at the base of the flowering stem, producing a new corm, on top of the old one, from a bud axillary to one of the leaves. One or more axillary buds at the uppermost nodes of the old corm also develop into new flowering shoots and eventually into new corms, so that the number of corms increases year by year by sympodial branching (Fig. 929). The corm scales are formed from the bases of the scale leaves which envelope the lower part of the flowering stem. The old corms rot away, leaving a space beneath the new ones, and into this space the new corms are pulled down by thick contractile roots, produced in late summer from the base of the new corm (see p. 814). The plant thus maintains a uniform depth in the soil. In the seedling the first corm is produced by the swelling of the hypocotyl.

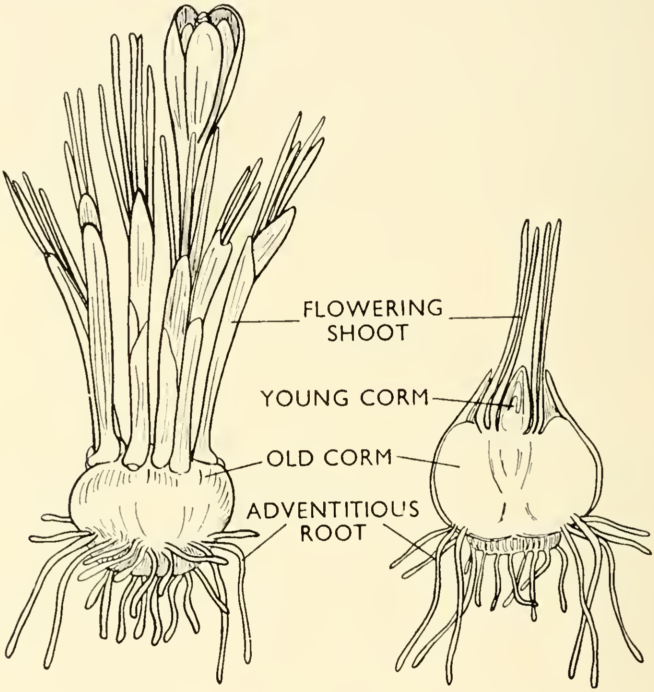


Fig. 928.—*Crocus sativus.* Diagram showing corm structure and the growth of aerial shoots from axillary buds on the upper part of the corm.

The corm of *Arum maculatum*, often cited as an example, is, however, plagiotropic and is really a very short rhizome. Although corms are not uncommon in Monocotyledons they are less common among Dicotyledons. Good examples in the latter class are the so-called Bulbous Buttercup (*Ranunculus bulbosus*) and species of *Corydalis.*

5. *Bulbs.* A bulb differs from a corm in that the stem is reduced to very small dimensions and the body of the bulb is made up of thick, fleshy bulb-scales. The difference is a question of proportion. In the corm the swollen stem is the main storage organ and the scales are merely protective, while in the bulb the scales themselves have been magnified and have replaced the stem as the main storage organs. The stem is no more than a thick disc or very flat cone, but it has an apical bud on the upper side, and adventitious roots are formed in an annual crop from the marginal portion of the underside, their development following a resting period of from two to four months after the conclusion of flowering. The fleshy scales are set very close together, and their bases of insertion almost or completely surround the stem. In *Tulipa* the bulb scales are formed independently of the foliage leaves, but in *Narcissus* they represent the persistent bases of the foliage leaves. In both cases, however, they are richly stored with food material (Figs. 930 and 931).

FIG. 929.—*Antholyza paniculata.* Group of attached corms showing their sympodial branching.

The bulb of *Lilium* differs from the above examples, chiefly in the much greater number and smaller size of its fleshy scales, the outermost being loosely arranged and easily detachable (Fig. 932). In favourable conditions these detached scales will produce adventitious roots and a bud which can grow into a plant.

The flowering bud for each year develops during the previous summer. In *Tulipa* the apex of each bulb becomes transformed into a flowering axis, but in *Narcissus* the apex itself persists and forms only a few foliage leaves, the flowering axis being axillary. The branching of *Tulipa* is thus sympodial, that of *Narcissus* is monopodial.

The organs of the flower are completely formed in the flowering bud by the end of summer, together with the rudiments of the foliage leaves, and

FIG. 930.—*Narcissus pseudo-narcissus.* Longitudinal section through a bulb with a lateral offset showing adventitious roots at the base and foliage shoot above.

FIG. 931.—*Nerine capensis.* Longitudinal section of a bulb showing leaf base scales and an offset developing from one of the axillary buds.

FIG. 932.—*Lilium candidum.* Bulb showing small loosely arranged scales.

only require to expand when the flowering season arrives. This expansion is carried out at the expense of material stored in the scales, which consequently shrivel, the outermost becoming dead and papery. After flowering the foliage leaves persist and the food material they elaborate is sent down to the bulb. In the Tulip this food promotes the development of one or more axillary buds into new daughter bulbs, which absorb the surplus of food from the old bulb and consequently replace it. In *Narcissus* the food is stored in the leaf bases, both of the current year and those persisting from the two or three previous years. An axillary bud also develops into a new flowering bud and one or more other axillary buds may develop into daughter bulbs which, however, do not replace the mother bulb, which remains active for years.

FIG. 933.—*Dentaria bulbifera.* Shoot with axillary bulbils.

The bulb of the Bluebell (*Scilla non-scripta*) is intermediate in character between the two examples given above. The scales consist of the bases of the foliage leaves of one year only but its growth is sympodial.

Among the Orchids we commonly find green bulbous structures at the base of the leaves, which are called **pseudo-bulbs**. These are really tuberous stem or branch segments, sometimes involving the whole length of the stem, sometimes only a single terminal segment, the apical bud of which aborts, but which bears one or two fully developed foliage leaves. A new shoot arises from the axil of a scale at the base of the pseudo-bulb, and this in its turn ends in another pseudo-bulb, so that the appearance is presented of a row of green tubers connected together at their bases by a slender stem bearing scale leaves.

There are numerous instances of the axillary buds on aerial shoots becoming transformed into small bulbs or **bulbils.** Good examples are shown by *Dentaria bulbifera* (Fig. 933) and *Lilium bulbiferum*, in which nearly all the axillary buds are so transformed. These bulbils are readily detached and form an effective means of vegetative propagation. In the genera *Allium* and *Agave* (Fig. 934) and in some alpine plants, *e.g.*, *Polygonum viviparum* and *Poa alpina*, the flowers are often transformed into bulbils, but the latter cases are undoubtedly related to the very short growth season available to the plants and perhaps to the scarcity of pollinating insects at high levels. Finally there is the case, described by Goebel, of *Cryptocoryne* (Araceae) in which the embryo itself becomes a bulbil and is shed naked, detached from its cotyledon, which remains in the seed. These latter cases of modification of floral structures, though not morphologically equivalent, are included under the biological term "vivipary," of which we shall say more when dealing with Mangrove trees in Volume IV.

FIG. 934.—*Agave americana.* Part of an inflorescence showing the replacement of flowers by detachable bulbils.

FASCIATED STEMS.

While it is not our intention to enter upon the bewildering study of plant abnormalities known as **Teratology,** there is one such abnormality of stems which we shall mention because of its frequent occurrence and striking appearance. It is that called **fasciation,** which consists of the development of a strap-shaped structure, often several inches broad, in place of a normal stem. Fasciated stems have a " growing line " instead of a growing point (Fig. 935). They often carry hundreds of leaves and enormous numbers of flowers. A second type, called ring-fasciation, transforms the stem into a wide cylinder, open at the top and lined with an internal as well as an external epidermis. A complete explanation of the morphology of these monstrosities is not available, but there are two theories, one being that there has been an enlargement of a single growing point and the other maintaining that there has been a congenital fusion of many shoots. Worsdell, in supporting the latter theory, claimed that it was due to a recrudescence of the primitive form of branching, dichotomy, otherwise scarcely known among Angiosperms, with the concrescence of the numerous shoots thus produced.

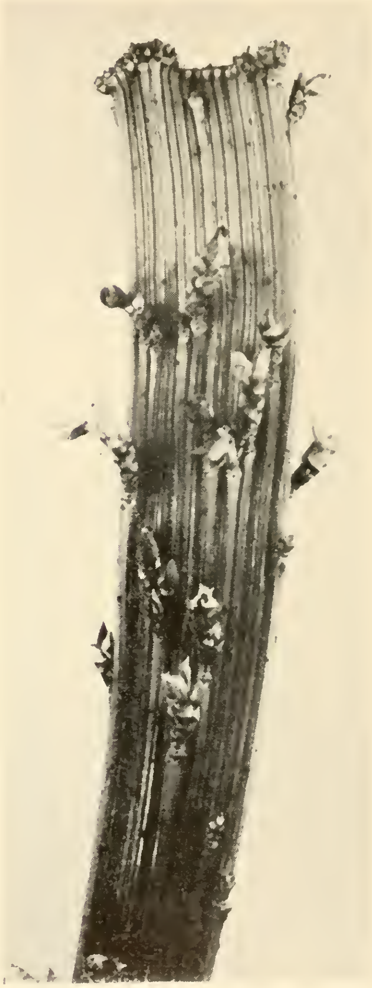


FIG. 935.—*Forsythia suspensa.* Upper part of a fasciated shoot.

Biologically there are two types of fasciation, one which is germinal and inherited and another which is somatic and non-heritable. Outwardly they are indistinguishable, but there is some evidence that the latter type is stimulated by insect damage to the growing point.

CHAPTER XXII

THE ANGIOSPERMAE: LEAVES

When we turn to the consideration of the angiospermic leaf we are confronted by the same difficulty of definition that we found in the case of the stem but in an accentuated degree, inasmuch as the range of morphological variation is much greater among leaves than among stems. Whatever formal definition of a leaf we attempt to frame, it will be possible to find some cases which appear to contradict it.

The science of comparative morphology, which arose from Goethe's famous " Essay on Metamorphosis," was based upon the concept of organ categories, to which we referred in the last chapter ; that is to say, on the principle that the plant body is built up of a limited number of kinds or categories of organ, primarily distinct from each other, but related, in the architecture of the plant, in a fundamentally uniform way, no matter how variable their external appearance may be. According to the principle of metamorphosis which Goethe formulated, any one kind of organ may vary, according to its position and function, so far from the normal that it may become difficult to recognise. Nevertheless it should not, so the argument runs, take over wholly the character of an organ of a different category, and it was considered to be the business of the morphologist to trace out and determine its true nature. So rooted did this idealistic theory become that controversies were carried on, sometimes without any acceptable conclusion, regarding the placing of such structures as the ovule in their proper category of leaf or axis. The most familiar type of leaf, namely the green foliage leaf, was tacitly assumed to be the ideal form, and all other " leaf " organs were supposedly metamorphosed foliage leaves.

With the growth of our knowledge of plant evolution such formal ideas of morphology have become obsolete. Goebel, in his great " Organography of Plants," was the first to break away from them by directing attention first and foremost to the functional aspect of organs and their relationships to the plant's conditions of life. He was careful, however, to avoid the naive adaptationism which confuses *post hoc* with *propter hoc* and seeks to relate every observed structure to some supposed function in relation to the environment. The complexity of plant structure is not necessarily a direct reflection of the complexity of the environment. Even with our limited knowledge of the life conditions of plants it is quite evident that similar requirements have been met by plants in an infinity of different ways, which are not physiologically predetermined. We must combine both the morphological and the physiological viewpoints if we are to attain a natural understanding of plant structures.

Are we then to abandon all categories and treat every plant structure as an independent entity? Not entirely so. A survey of the types of lower plants, such as we have made in former chapters of this work, shows us that the categories of stem, root and leaf in the Higher Plants are not primitively distinct but are differentiated from one primary structure, the axis, which, as we have previously suggested, may be derived from the primordial cell-filament. They have been differentiated moreover in very many ways and in very various degrees, so that fine-drawn distinctions between them must be artificial. Nevertheless, if we compare many types of Higher Plants we find certain regularities in the relationship of organs, associated with the greatest diversity of individual form, which justifies us in using the old categories as general descriptive terms, although without their old rigidity, and thus simplifying and clarifying our ideas, while leaving room for the recognition of cases which cannot be fitted into the framework of any formal definition.

We have already applied this principle of relationship when we described the stem as the organ which bears the leaves. What then are we to include under the term "leaf"? We may agree to apply the term to those structures which arise as lateral outgrowths from the superficial tissues of the stem without any subtending organ, and are arranged in a definite geometrical order. Further, we may add as normal, though not invariable characters, that leaves are generally of bilateral symmetry and of limited growth, that they subtend buds in their axils and that they do not directly bear other leaves though they may produce buds. Thus, if we seek to apply the name to a particular organ we must be guided by the generality of its characters, recognizing that Nature has no regard for our subjective limitations, and that a given organ may contravene one or even several of the above characters and yet be most appropriately classified as a leaf.

Much was made at one time of the restriction that a leaf could never be terminal on the axis. There are a number of instances, both normal and abnormal, in which leaves do assume this position by displacing or replacing the true stem apex. Apart from such disputable structures as carpels or stamens, which are frequently terminal, there are terminal leaves in *Polygonatum*, which owe their position to the abortion of the apical bud. Among the Gymnosperms, *Pinus monophylla* also appears to have its single leaves terminal on the spurs. Yet in this case also, traces of an abortive apex may be found, so that the terminal position is only secondary. In *Juncus*, "terminal" leaves may cover and include the stem apex in their bases, but they do not replace it. Instances which have also been cited in *Corydalis* and in a Bamboo appear to be similar to the foregoing, *i.e.*, the apparently terminal leaves have sheathing bases enclosing the stem apex, which is moreover abortive. In fact no case has been produced in which the stem apex is directly transformed into a terminal leaf and until this can be shown we may continue to treat leaves as characteristically lateral organs.

When we consider the phylogeny of the angiospermic leaf we find that it shares with the pteridophytic leaf a character which is of wide significance, namely that its vascular supply leaves a gap in the vascular system of the stem, which stamps it as belonging to the same megaphyllous cycle of affinity. This structural condition is called **phyllosiphonic,** in contrast to the **cladosiphonic** condition in which only the branch-traces leave gaps in the stem stele, a condition which is characteristic of the Lycopodiales and other microphyllous groups. In Chapter XVI we have seen that the megaphyllous leaf may have been evolved from a flattened branch-system bearing microphyllous leaves, whose small separate laminae became merged into a larger general lamina. This evolutionary scheme, which is associated with the names of Lignier, Tansley and others, harmonizes with the apparent derivation of both microphyllous and megaphyllous stocks from primitive, leafless types like the Psilophytales, with dichotomous axes, (see p. 650) and it has much to commend it. Among the Psilophytales we find types which are covered with minute leaves, developed apparently like superficial emergences, which invite comparison with the microphylls of both Mosses and Lycopods. If we accept the homology of these leaf types we must regard the microphyllous state as the more primitive of the two and the megaphyllous state as derived from it.

From the pteridophytic leaf, through the gymnospermic to the angiospermic leaf, the fundamental type has not altered, though specialized growth patterns have brought about many changes of form. One rather marked difference may be observed in the vein systems, or **venation.** In Ferns an " open " dichotomous venation is characteristic, in which the branching of the veins is open towards the leaf margins, while in Angiosperms the lamina is usually pervaded by a vein-network with closed meshes. We shall return to this subject later (p. 957).

We have previously quoted examples of both rootless and stemless plants, but if we consider the formative importance of the leaf in the architecture of the stem, which we have outlined in the last chapter, it is scarcely surprising that the existence of a truly leafless plant is doubtful. There are of course, very many plants in which the leaves have been reduced until they are no more than scales, yet these cannot be considered as other than metamorphosed leaves. Scales may be reduced almost to invisibility, as on the rhizome of the saprophytic Orchid *Corallorhiza innata*, or they may have lost even a vascular supply, as in *Cuscuta*, and consist only of undifferentiated parenchyma, but they are, nevertheless, so clearly linked by intermediate forms with larger and better developed leaves, that we must regard them as leaves in spite of their extreme reduction. If we exclude floral leaves and speak only of vegetative structures, the nearest approaches to a truly leafless condition are to be found in the following : (1) the early stages of the parasite *Orobanche*, which has no vestige of leaves or of an apical bud, until it has become well established on its host plant (Fig. 936) ; (2) the cylindrical green stems of *Heleocharis* and *Scirpus lacustris*, which consist of a single, greatly extended internode, bearing only (in the sterile state) two small scales at the apex ; (3) the cladodes of *Asparagus*, if so extreme a case may be admitted, can also be cited as leafless stems, though of a very reduced kind.

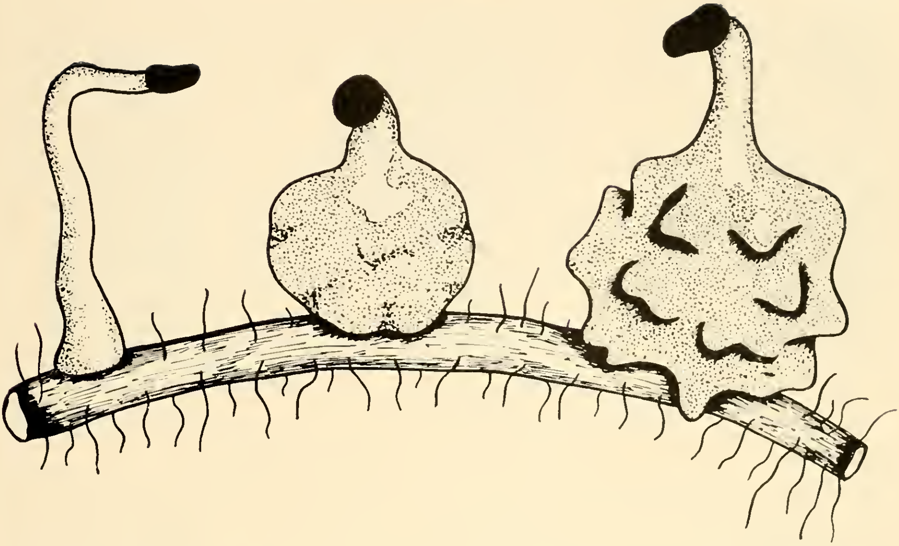


FIG. 936.—*Orobanche ramosa.* Seedlings showing leafless tuberous stems. (*After Goebel.*)

LEAF FORM.

Both in external form and in internal structure leaves are exceedingly variable, more so perhaps than any other plant organ. This is partly due to physiological necessity, for the leaf, on account of its relatively large surface and exposed position, is intimately affected by climatic variations; indeed it is in this respect the most sensitive part of the plant. Moreover the structure of every leaf embodies a compromise between two opposed requirements, namely, the necessity for the effective exposure of as large a surface as possible to sunlight, which is required for photosynthesis, and the necessity for protection against excessive evaporation, to which its large surface and thin texture make it peculiarly liable.

On the other hand a great deal of leaf variation has nothing to do with physiological causes but is functionally indifferent and is referable to heredity. Such are the manifold variations of leaf outline and appearance, which are often so closely connected with the systematic relationships of the plants concerned, that is to say, with their genetical history, that they are of the greatest value as aids in identification. A useful distinction has been made in calling physiologically determined plant forms **ecads** and hereditary forms **phyads,** and the difference is genuine and deep-seated.

Variations which are clearly related to special environmental factors, as in the case of aquatic or of desert plants, we shall deal with under Bionomics in Volume IV. Here we shall consider only the systematic variations.

In earlier days when Botany was largely a classificatory science, the forms of leaves were recognized as important guides to affinities. They were, therefore, intensively studied and classified under a large number of types with descriptive names. At the present day this kind of study is chiefly of interest to the systematist and students are not often introduced to the rather bewildering assortment of terms employed. The study of systematics is, however, regaining some of the ground which it lost during the post-Darwinian era, for it has been realized that systematic relationships are an essential part of a plant's being and are often valuable guides in problems of physiology, ecology, and above all of genetics.

We present, therefore, a simplified and illustrated classification of leaf forms which covers the main types. If any student is inclined to cavil at such a multiplicity of technical terms let him reflect what would be the difficulty of describing these variations or indeed any organic forms without their aid. Botanical terminology has been evolved to lessen labour, not to increase it, as some are apt to suppose.

Leaves are classified, in the first place, as either **simple** or **compound.** A simple leaf may have a divided or undivided lamina, but in the former case the portions of the divided lamina are not wholly separated from each other or from the midrib of the leaf. A compound leaf is composed of separate leaflets, each of which has a separate and distinct base, attached to a common leaf stalk, and each may have a small secondary leaf stalk of its own.

Either type of leaf may have a stalk or **petiole,** which carries the blade or **lamina.** Alternatively the leaf may be **sessile,** that is, attached directly to the stem at the base of the lamina, with no intervening petiole. When the base of a sessile leaf surrounds the stem at the node, it is called **amplexicaul.** When an amplexicaul leaf is extended beyond the stem on the far side of the node, so that the stem appears to be growing through the leaf, it is called **perfoliate.**

If the lamina of a sessile leaf is prolonged downwards from the point of attachment at the node, so that it forms a membrane or frill, attached to the stem, the leaf is said to be **decurrent.** When two sessile leaves stand opposite each other at a node, and their bases are joined to each other round the stem, they are called **connate.**

The divisions of the lamina, whether in simple or in compound leaves, may be arranged either in two series, on each side of a common axis, in which case they are said to be **pinnate** ; or they may form a radiating series like the fingers of a hand, in which case they are called **palmate.** In a simple pinnate leaf the common axis is the midrib of the leaf, but in a compound leaf it is a prolongation of the petiole called the **rachis,** as in the compound leaves of Ferns. A pinnate leaf with an even number of paired leaflets is said to be **paripinnate,** but if there is an odd terminal leaflet it is called **imparipinnate.**

If the margin of a leaf is smooth and without indentations it is said to be **entire,** while the various degrees of indentation, with their names, are illustrated in Fig. 937. A distinction is drawn between indentations which reach to the midrib, thus dividing the lamina into separate portions, and the less marked divisions which leave a continuous portion of the lamina along

FIG. 937.—Types of leaf margins. A, Entire: *Diervilla*. B, Sinuate; *Quercus*. C, Dentate; *Platanus*. D, Serrate; *Campanula*. E, Biserrate; *Ulmus*. F, Spiny; *Ilex*. G, Crenate; *Melittis*. H, Incised; *Crataegus*. J, Ciliate; *Cerasus*.

the middle portion of the leaf. The former are described as **pinnatifid** or **palmatifid** and the latter as **pinnatisect** or **palmatisect** respectively. These and certain other special types of division in simple leaves are illustrated in Figs. 938 and 939.

Fig. 938.—Types of Pinnate division in simple leaves. A, Runcinate; *Taraxacum.* B, Pinnatifid; *Senecio vulgaris.* C, Pinnatisect; *Papaver.* D, Bipinnatifid; *Senecio jacobaea.* E, Bipinnatisect; *Achillea.* F, Lyrate; *Lapsana.*

The common forms assumed by compound leaves are shown in Fig. 940. Some of these are complicated by a higher degree of subdivision than simple pinnation, the pinnae being themselves divided into **pinnules** and these again, sometimes further subdivided, producing **bipinnate** or **tripinnate** types.

Variations in the relative length and breadth of simple leaves are illustrated in Fig. 941. The narrowest leaves, such as those of grasses, with parallel sides, are called **linear** while other varieties are given in the Figure, together with some of the principal variations in the attachment of leaf and stem, as described above.

The peculiar form of leaf called **peltate** deserves a special mention. This is a mushroom-shaped structure with the petiole apparently attached at or near the middle of the underside of the lamina. In many cases (*e.g. Hydrocotyle vulgaris* and *Cotyledon umbilicus*) the seedling plants show a series of stages illustrating that the mature peltate leaf has developed from a cordate form, the basal lobes of which have coalesced so as to produce an orbicular outline.

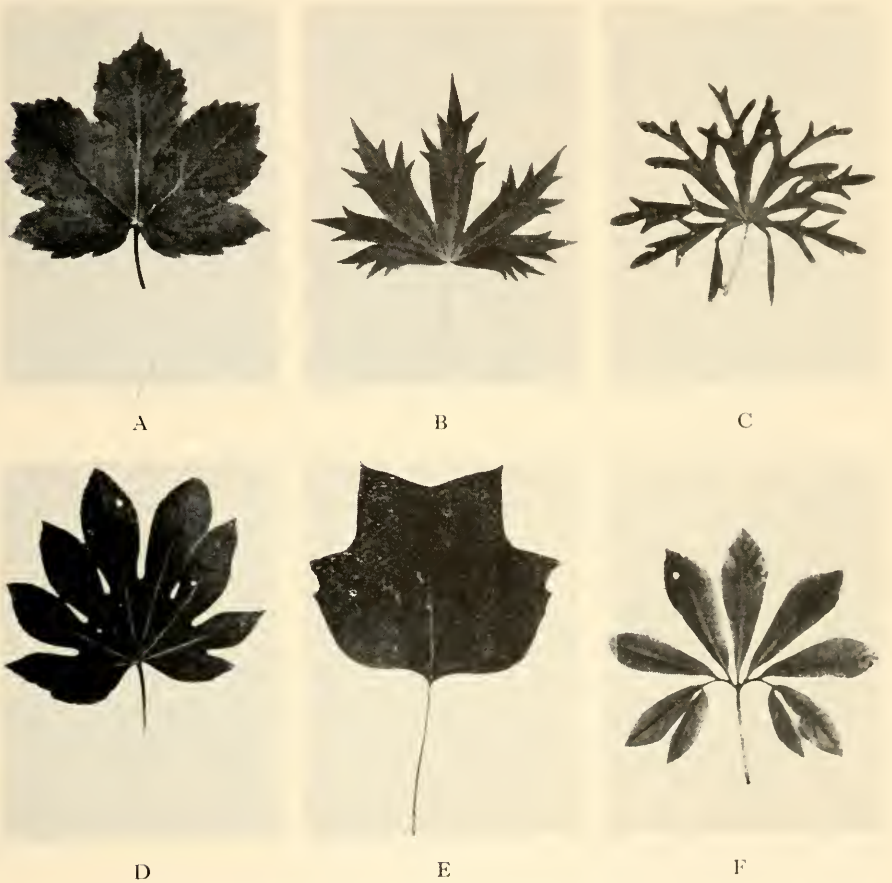


Fig. 939.—Types of Palmate division in simple leaves. A, Palmate ; *Acer*. B, Palmatifid ; *Delphinium*. C, Palmatisect ; *Geranium*. D, Palmatilobed ; *Fatsia*. E, Emarginate ; *Liriodendron*. F, Pedate ; *Helleborus*.

The size of the leaves on any individual plant is characteristic of the species and does not vary very widely, for leaves are organs with limited growth and the size ultimately reached depends chiefly on hereditary factors. Some differences of size exist between young and old plants and between those growing in the shade and in the sun. Young plants and young shoots, such as the stool-shoots which spring from the base of a bush or tree that has been cut down, may produce leaves of unusually large size, owing to their greater vigour of growth. The size of leaf steadily diminishes with age, although, as we have remarked, the range of such individual variation is not great. It has been remarked that the size of the meshes, in leaves with a network of veins, likewise diminishes with age, this being one of the few points in which plants show a distinct morphological change due to senescence.

Fig. 940.—Some common forms of Compound leaves. A, Pinnate ; *Onobrychis.* B, Bipinnate ; *Acacia.* C, Tripinnate ; *Anthriscus.* D, Ternate ; *Choisya.* E, Biternate ; *Aquilegia.* F, Digitate ; *Lupinus.*

On the other hand, the variation of size between different species is immense. Putting on one side the numerous cases of leaves which are reduced to scales, many of which have been diminished almost to the vanishing point, and considering only green foliage leaves, the largest known leaves are many thousand times the size of the smallest. These differences are to some extent related to the conditions of the environment, for larger leaves are usually capable of a greater evaporation of water than small ones, in proportion to their greater surface. Raunkaier has devised an ecological classification of

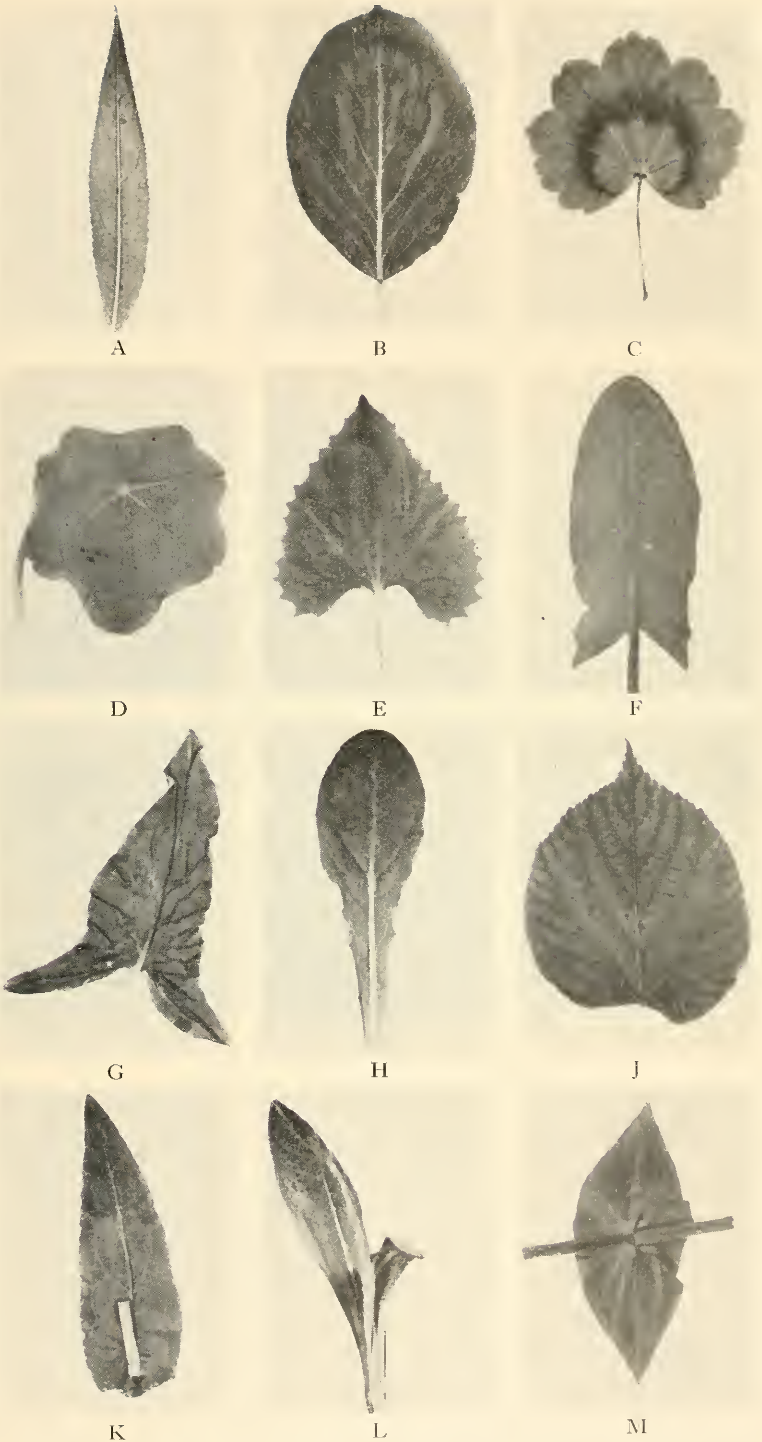


FIG. 941.—Variations of leaf form in Simple leaves. A, Lanceolate ; *Salix.* B, Ovate ; *Pyrus.* C, Orbicular ; *Pelargonium.* D, Peltate ; *Tropaeolum.* E, Cordate; *Doronicum.* F, Sagittate ; *Rumex acetosa.* G, Hastate ; *Arum.* H, Spatulate ; *Calendula.* J, Acuminate ; *Tilia.* K, Amplexicaul ; *Rumex crispus.* L, Decurrent ; *Verbascum.* M, Connate ; *Blackstonia.*

plants on the basis of leaf size, as we shall see in Volume IV, and has shown that the predominance of leaves belonging to one or other of these size-classes in a given habitat is indeed an expression of the prevailing conditions. Nevertheless it must not be overlooked that the production of a very large number of small leaves may, to a great extent, compensate for their smaller size, so that the total area of foliage possessed by such a plant may be scarcely inferior to that of a plant with a smaller number of larger leaves. Thus any advantage in regard to a lower rate of water loss, assumed to be gained by the smaller size of leaf, may be neutralized by their greater numbers.

There is, indeed, a principle of compensation to be observed in this connection, for, as we remarked in the last chapter, plants which are richly branched tend on the whole to produce smaller leaves than those which have little or no branching. The largest leaves of all are, in fact, produced by the unbranched stems of Palms. Kerner cites as the largest leaf on record, that of the Palm, *Raphia taedigera*, of which the petiole is 4 to 5 metres long while the blade may measure 19 to 22 metres in length by 12 metres in breadth. Although no Dicotyledon can rival this giant, the palmatifid leaves of *Gunnera manicata* may reach a diameter of $2\frac{1}{2}$ to 3 metres, with a petiole of about equal length. The floating leaves of the South American water-lily, *Victoria regia*, are also among the largest known and in its native Amazon may measure nearly 4 metres across (Fig. 942). Exceptionally large leaves such as these are rarely, if ever, produced on aerial stems. They usually spring from short underground stems of tuberous form, commonly, though erroneously, called " root stocks." Leaves of whatever size which thus appear

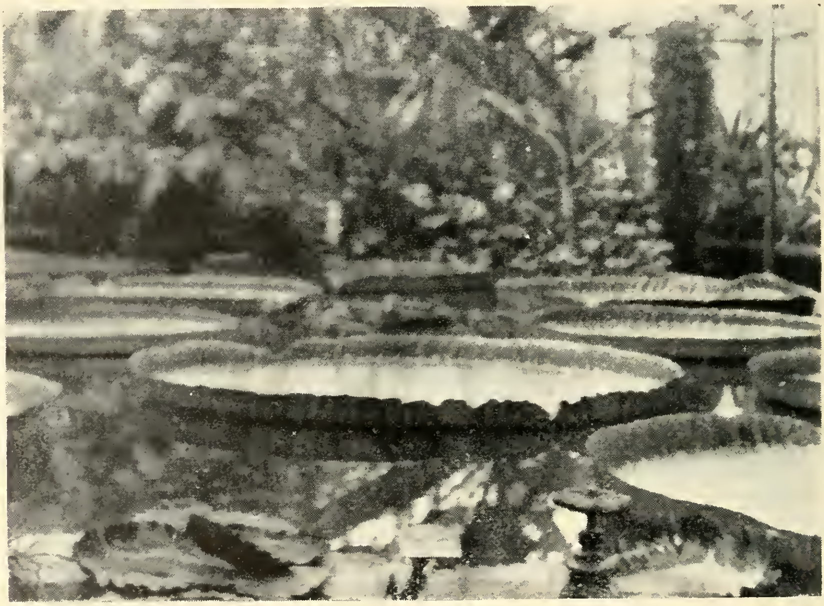


FIG. 942.—*Victoria regia.* Floating leaves. Kew Gardens.

to come directly from the ground are classed as **radical leaves**. They are specially frequent among Monocotyledons, but are also characteristic of dicotyledonous biennial plants, in which the aerial stems only emerge from the ground level and elongate during the second year of life.

VENATION OF LEAVES.

The term " vein " is often used as if it were synonymous with a vascular bundle. This is only true of the smaller veins, for the midrib and the larger veins of the leaf may contain a group of vascular bundles and sometimes indeed have a structure which closely resembles that of a stem. Moreover, when the leaves of certain plants, such as *Begonia* or *Torenia* are employed as cuttings, and inserted in the soil until they develop adventitious buds and roots, the growth of these new organs may stimulate development in the larger leaf veins, leading to the formation of quite considerable amounts of secondary wood, arranged in a circular zone, exactly as in a stem.

These anatomical resemblances have been used as arguments in favour of the axial nature of the leaf, a question, however, which we have already sufficiently discussed (see p. 947).

The larger veins are usually encased in a sheath of parenchymatous or sclerenchymatous cells which cuts them off from the mesophyll. These sheaths are generally more developed on the lower than on the upper side and consequently they stand out as more or less prominent ribs on the lower leaf surface, though less commonly they may also protrude above the level on the upper surface. The smaller veins, on the contrary, are in close contact with the mesophyll tissue.

Veins serve both mechanical and conducting functions in the leaf, as in the stem. In many leaves, especially in Monocotyledons with very long leaves, the sclerenchymatous sheaths of the veins are extremely strong and they are thickest above and below the vascular bundle of the vein, presenting, with the latter between them, a girder section which is very resistant to bending strains.

It is generally said that the venation of the leaves in Monocotyledons and Dicotyledons is quite distinct. The monocotyledonous leaf is usually broad-based and clasps the stem at the node. It receives a considerable number of leaf trace bundles from the stem, and these form veins which follow a more or less straight and parallel course towards the apex of the leaf (Fig. 943), though in leaves which are broad in the middle part, the veins may be markedly bowed outwards and form a series of parallel arcs. The dicotyledonous leaf has usually a very limited number of trace bundles, which branch repeatedly in the lamina and anastomose to form a network. The variety of patterns is very great and seems to be determined more by factors of heredity and relationship than by immediate physiological needs.

In Monocotyledons there are relatively few cross-connections between the main veins, and such as there are follow a straight transverse course from vein to vein (Fig. 944). The network in the Dicotyledon, however,

FIG. 943.—*Convallaria majalis.* Leaf showing parallel venation.

FIG. 944.—*Aponogeton fenestrale.* Leaf in which the lamina is reduced to thin sheaths around the veins. This leaf shows the transverse connections between the parallel main veins which are characteristic of Monocotyledons.

FIG. 945.—*Ilex aquifolium.* Part of a leaf skeleton showing the reticulate venation and the numerous free bundle-ends.

provides a great number of alternative paths for the flow of liquids and the mesophyll is much more richly supplied with conducting tissues than in the other group. Moreover, the meshes of the net nearly always enclose at least one branch vein which ends blindly in the middle of the mesh-space, thus ensuring that no part of the mesophyll is more than two or three cells distant from a vascular bundle (Fig. 945).

The greater physiological efficiency of the dicotyledonous type of venation is clearly seen if a leaf of both types is partly cut across transversely. In the Monocotyledon the severing of the main veins practically cuts off the water supply to the portion of the lamina above the cut, and in dry weather it will wither. In the Dicotyledon, however, the danger of such physiological isolation scarcely exists, so long as some of the principal veins remain intact. Notwithstanding the general difference between the two groups in this character of venation, it is not an absolute distinction. There are some Dicotyledons (*e.g.*, species of *Eryngium*) with parallel venation in narrow leaves, which look typically monocotyledonous (Fig. 946). On the other hand the large monocotyledonous family of Araceae, among others, has leaves with a broad lamina and network venation (Fig. 947).

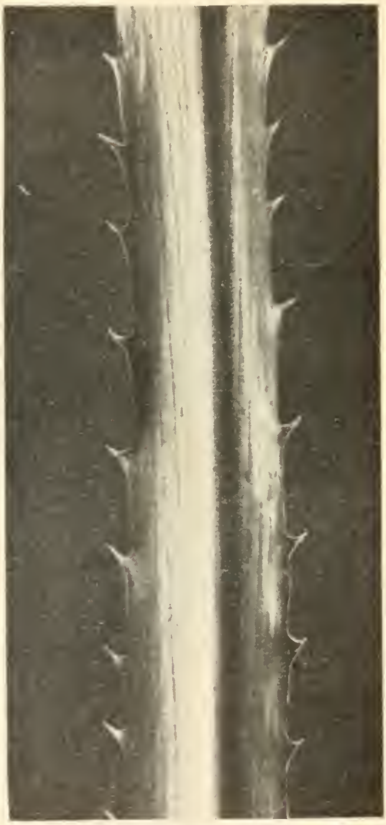


FIG. 946.—*Eryngium agavifolium.* A dicotyledonous leaf with parallel venation.


FIG. 947.—*Colocasia antiquorum.* Monocotyledonous leaves with a broad lamina and reticulate venation.

The difference is probably not truly based on systematic affinity, but rather on the type of the leaf in each case. That Monocotyledons show that such a high degree of uniformity may be due, as we shall see below, to their leaves being in reality phyllodes, or flattened petioles, with a venation which is characteristic of petioles or leaf bases rather than of true laminae. The same is probably true of reduced leaves, such as bracts and bud scales, which usually show a simple and parallel type of venation even in Dicotyledons.

The variety of patterns displayed by net-veined leaves is due, at least in the principal features of the pattern, to differences in the mode of growth of the leaf blade. In some families the pattern is so constant that it forms a useful character for recognition. In other cases there may be variation even in different leaves of the same plant, a notable instance being the contrast between the floating leaves and the submerged leaves of many aquatics.

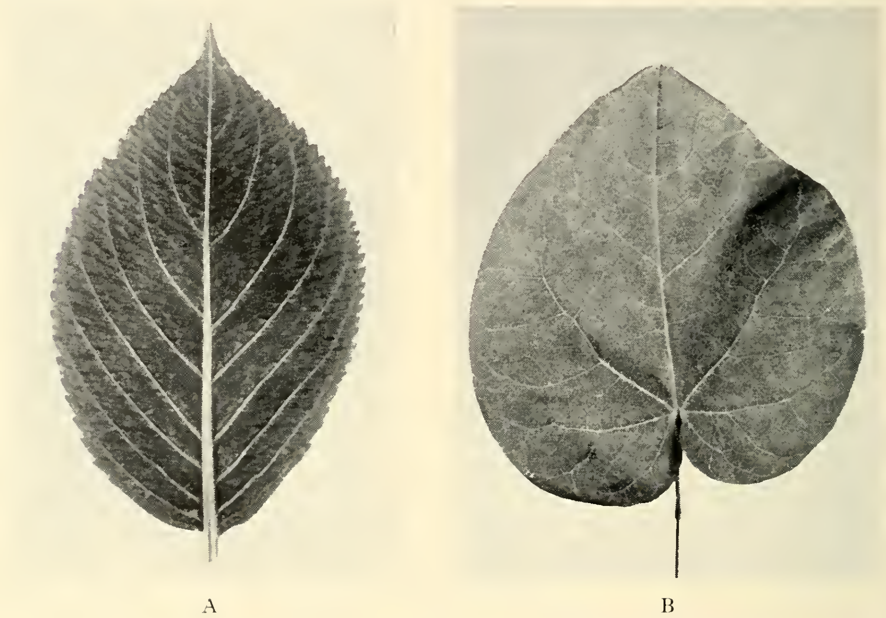


Fig. 948.—Pinnate and palmate venation. A, Pinnate; *Hydrangea*. B, Palmate; *Cercis*.

It has been observed by Zalenski that age affects the leaf structure. Comparing mature leaves produced earlier and later in the development of a plant, the latter have smaller cells and consequently the vein islets are smaller and the stomata and hairs are closer together. This is one of the few examples of senescent changes of structure in plants.

Two main varieties of pattern may be mentioned, namely pinnate and palmate venation (Fig. 948). The former has a single midrib from which the chief branches are given off in pinnate order. The latter usually has several main veins springing from the upper end of the petiole and spreading out fanwise. While both types are frequently associated with leaves which show the corresponding type of division of the lamina, they may also occur in entire leaves, being determined by the growth pattern of the leaf as a whole.

HETEROPHYLLY.

It is no uncommon thing to find leaves of different types on one and the same plant, a phenomenon known by the general name of **heterophylly**, although the features of the condition are by no means uniform. In the widest sense of the term, and including as leaves all the various categories of bracts, cataphylls, etc., one might say that heterophylly is the universal rule, but confining ourselves only to modifications of the foliage leaves, we may distinguish at least three main types of heterophylly. The first type we may call **environmental heterophylly**, because the difference is conditioned by environmental factors. The clearest examples of this are to be seen among water plants, where the submerged and the floating or aerial leaves may be very distinct. Among dicotyledonous aquatics the submerged leaves are often so much subdivided that their segments are reduced to mere filaments, while the aerial leaves have a fully developed lamina (Fig. 949). Monocotyledonous aquatics on the other hand frequently have linear submerged leaves with no lamina. Certain plants, especially shrubs growing in dry climates, may also show a variation of leaf form according to the season, the normal leaves only appearing during the rainy season and being substituted by scale-leaves during the dry part of the year. We shall refer to these environmental relationships in Volume IV. Closely associated with the above instances are those in which certain leaves are specially modified from the normal type in connection with some special function, such as

FIG. 949.—*Ranunculus peltatus.* An example of environmental heterophylly. The submerged leaves are filamentous.

water or food storage, climbing or the capture of insects. Some adaptive modifications of this type we shall deal with later in this chapter.

The second type or **habitual heterophylly** involves the formation on the main shoots, of foliage leaves of different sizes, and to a lesser extent, of different shapes, apparently without any special functional significance. Among the commonest cases of such pure heterophylly are those of plants with opposite leaves in which one leaf of a pair is smaller than the others. This is quite common on plagiotropic* shoots, where it is normally the upper leaves which are reduced in size. This is most pronounced in those species where the leaves on plagiotropic shoots are twisted laterally, so as to form flattened shoots on which there are two lateral rows of large leaves, and two dorsal rows of small leaves, representing unequally developed leaf-pairs. This lateral heterophylly may perhaps confer an advantage by avoiding the overshadowing of leaves by other leaves but it is not inseparable from this condition, because habitual heterophylly is also found on the orthotropic shoots of many plants where the factor of overshadowing does not come in. The reduction of one member of each pair of leaves often goes so far as its complete disappearance, the originally opposite leaf arrangement being sometimes traceable by the presence of supernumerary stipules at each node and sometimes, as in the Elm, traceable only during the development of the young plant, in which a primitively isophyllous, opposite arrangement of the leaves gives place, at an early stage, to an alternate arrangement with leaves in two ranks only, through a short intermediate zone of true heterophylly. These latter cases are of particular interest in that they suggest the possibility that alternate leaf arrangements in which no trace of the change now remains, may have been derived from the opposite arrangement.

A very marked, but exceptional, type of habitual heterophylly is exhibited by certain plants which bear leaves of variable form, distributed at random. Three well known examples of this are : *Broussonetia papyrifera*, (the Paper Mulberry), *Artocarpus integrifolia* (the Jack Fruit) and *Lonicera japonica*, the last named producing irregularities especially under starved conditions. In all these cases the normal leaf shape is entire, but only a minority of the leaves retain this form, the majority developing in most irregular fashion, various parts of the lamina being suppressed, so that hardly any two leaves are alike (Fig. 950).

Before leaving this type of heterophylly we may also mention cases where, as in the common Ivy, the leaves of flowering shoots, although retaining the full size and character of foliage leaves, differ in outline from those of vegetative shoots. Such differences probably merge into the widespread condition of the production of specialized bracts associated with the flowers.

The third type or **developmental heterophylly** is that associated with the change from juvenile to mature foliage in the development of the individual. This touches upon the vexed question of evolutionary recapitulation during ontogeny, but with a few exceptions the changes involved are not such as

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* The term **plagiotropic** refers to shoots of horizontal growth. The opposite term, **orthotropic**, refers to shoots of vertical growth.

to throw much light upon the evolution of the species concerned, certainly not, at any rate, in regard to their remote ancestry, though they may indicate comparatively recent changes of foliage type in the history of the race.

The case of the Ivy, mentioned before, may be considered as falling into this class, inasmuch as the palmate leaves, arranged in two ranks, which are produced on the climbing vegetative shoots, are naturally characteristic of the earlier stages of development, while the entire ovate leaves of the flowering shoots are only produced when the flowering stage has been reached. It is preferable, however, to regard the change in this case as correlated with bract development, which is in every case associated with the flowering stage of the plant, rather than as purely a phenomenon of maturity, for if flowers are not produced, no change of foliage occurs.

FIG. 950.—*Artocarpus integrifolia.* Leaves of various shapes, illustrating habitual heterophylly.

Juvenile foliage which gives place to mature foliage in the ordinary course of vegetative development is well known in *Pinus* (see p. 690) and some other conifers and occurs also in many Angiosperms, especially among woody climbers. The genus *Pothos* (Araceae) provides a very striking example. Starting with sessile, entire leaves in the young plants, there is first a change to petiolate leaves and later to divided leaves, which are only irregularly incised to begin with, but finally become regularly multipinnate. So great is the difference that young specimens in cultivation have been regarded as types of a new genus until their mature foliage appeared, in the same way that juvenile forms of some Conifers are vegetatively propagated and cultivated under the names of *Prumnopitys* and *Retinospora*, which are applied only to these juvenile states.

The genus *Eucalyptus* consists of large, rapidly growing tree species, which show a very marked difference between the juvenile and the mature foliage (Fig. 951). The later leaves hang vertically; they are always narrowly lanceolate, alternate and petiolate. The juvenile leaves, on the other hand, are variously shaped ; frequently obtuse, sessile, or even connate in pairs, and standing out stiffly from the branches (Fig. 952). The difference is so marked that one could easily believe that the mature shoots belong to some other species grafted on the juvenile tree. Almost equally marked, though less spectacular changes of leaf shape may be seen in many herbaceous plants such as *Campanula rotundifolia* (the Harebell), *Malva moschata* (Fig. 953), and in several species of *Scabiosa*, in which the juvenile leaves are entire and the mature leaves are deeply divided. In many plants, indeed perhaps in most, there is some degree of change in leaf form, from node to node. The rate of this change, which is genetically controlled, has been used as an index of the physiological maturity of the shoot.

FIG. 951.—*Eucalyptus sp.* Young trees showing juvenile foliage below and mature foliage above.

Certain species of *Acacia* develop only phyllodes (*i.e.*, flattened petioles) in the mature state but produce the typical multipinnate leaves of the genus on their seedlings. The change over takes place through intermediate stages, marked by progressive broadening of the petioles and the reduction and final

FIG. 952.—*Eucalyptus globulus.* A, Juvenile leaves. B, Mature leaves.

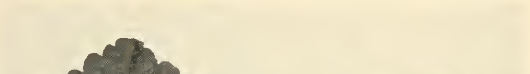

FIG. 953.—*Malva moschata.* Leaves showing successive forms from the orbicular juvenile leaves to the pinnatifid mature leaves.

disappearance of the pinnae. Here, at any rate, we seem to see a case of recapitulation of an evolutionary change, since the pinnate leaf is almost certainly the primitive type for the genus, which has been replaced by the specialized phyllode formation. The same replacement of laminar leaves by phyllodes can also be seen in some species of *Oxalis*, where the primary leaves are ternate.

Juvenility of foliage is not entirely confined to seedlings, for in many trees similar changes of leaf type may be seen on the vigorous stool shoots that spring from the base of felled individuals. Arising as they do in most cases from dormant buds formed when the tree was young, they frequently display juvenile characters and recapitulate changes observable in the seedling development.

Along with heterophylly there may be mentioned the asymmetry of leaves which prevails in certain plants, in which the two halves of each leaf, or the two sides of a pinnately compound leaf, are unequally developed. This may occur, as in the Elm, even on orthotropic shoots, but it is much more frequent on plagiotropic shoots. In the latter case it is often associated with dorsiventrality of the plagiotropic axis itself. The genus *Begonia* provides examples of this in nearly every species, but the relationship to the axis varies, sometimes the larger and sometimes the smaller half of the leaf being upwards. In the latter case, however, the larger half is usually turned upwards by secondary twisting of the leaf-stalks. Experiment shows that asymmetry can easily be induced in leaves by severing a vein on one side of the young leaf and thus reducing its nutrition, and in the naturally occurring examples an analogous difference of nutrition seems to be operative, the larger leaf-half being formed towards the better developed side of the dorsiventral axis, from which its trace bundles come. When stipules are present in such cases they are also often asymmetrical, the larger of the two being on the larger side of the leaf.

Asymmetry has been interpreted as an adaptation to minimise the overshadowing of each other by closely set leaves. It may have such a value in certain cases, but in orthotropic shoots with widely spaced leaves this need does not arise, nor can it in any case, be regarded as the cause of the asymmetry. Nevertheless the avoidance of overshadowing has a definite biological value, especially with plants growing in poor light. Many plants, especially those with plagiotropic shoots (Fig. 954), whether creeping, climbing, or woody, do in fact place their leaves, by the twisting of the petioles and by differential growth of the petioles in length, in the positions of minimum overlap. This fitting of the leaves together has been given the name of the **leaf mosaic** and some ecological importance has been attributed to it (Fig. 955). Apart from plagiotropic shoots, the basal rosette of leaves in biennials, (Fig. 956) the so-called " radical leaves," often show very well-marked mosaics, the petioles of the lower leaves in the rosette being so much elongated that their laminae are carried outwards beyond the laminae of the upper leaves. The leaves produced on the elongated flowering shoots produced later by the same plants may not, however, show any mosaic arrangement, unless they happen to be unusually large or closely placed on the stem.

In treating of adjustments of leaf position mention should be made of

FIG. 954.—*Cotoneaster horizontalis.* Plagiotropic shoot showing mosaic with leaves in two ranks.

FIG. 955.—*Hedera helix.* Mosaic of leaves growing on a shaded wall. The ability of the Ivy to grow in deep shade is favoured by its effective mosaic.

FIG. 956.—*Bellis perennis.* Rosette of radical leaves showing mosaic arrangement.

the peculiar change called **resupination**, or turning of the leaf upside down, which is most familiar in *Alstromeria* (Fig. 957). No definite advantage can

FIG. 957.—*Alstromeria aurantiaca.* Leaves showing basal resupination.

be indicated for this peculiar change, which is habitual in the genus, but in other cases the twisting of the leaf may have an ecological significance. Such are, for example, the "compass plants" of the American prairies, tall Composites (*e.g.*, *Lactuca scariola*) which place their leaves pointing north and south with the edges vertical (Fig. 958). In this way they receive equal lighting on both sides of the leaf, which has, correspondingly, an equifacial structure, both sides being alike. Similar twisting movements may also occur temporarily in plants exposed to very strong sunlight (Fig. 959), while in *Eucalyptus*, although the twisting into the vertical position is permanent it occurs only in the elongate mature leaves and not in the rounded juvenile foliage.

Fig. 958.—*Lactuca scariola*. A compass plant showing the north and south alignment of the leaves with thin edges vertical. (*Photograph taken in Chile.*)

LEAF FOLDING.

The young leaves which are still enclosed in a bud often show remarkable foldings due to the tight packing imposed by limitations of space (Fig. 960). This is not usually a mere crumpling of the young lamina, such as one might

FIG. 959.—*Coleus blumei.* Plant showing leaves with edges vertical, in strong sunlight.

FIG. 960.—*Brassica oleracea* var. *gemmifera.* (Brussels Sprout.) Longitudinal section through a bud to show the packing of the young leaves.

expect to arise from the independent growth of each lamina within the limits of the bud, but is evidently the result of co-ordinated growth, the manner of which is not yet understood. The particular type of folding is remarkably constant in each species and is known as the **ptyxis**. The variety of such arrangements is very great. In Monocotyledons the conditions are usually relatively simple, the leaves being either tightly rolled together into a single bundle or else folded together oppositely. The large leaves of the Palms are an exception, for they are often complexly pleated like a folded fan. In Dicotyledons individual rolling or folding or pleating, or combinations of these, are all known (Fig. 961). The mode of unfolding, when the bud begins

FIG. 961.—*Quercus robur.* Transverse section through a winter bud surrounded by protective scales and showing the pleated arrangement of the young foliage leaves within.

FIG. 962.—*Populus candicans.* Vernation showing rolled young foliage leaves and expanded bud scales at the base.

to grow, depends naturally on the particular ptyxis, and the appearance and relationships of the young leaves at this time are called the **vernation** (Figs. 962, 963 and 964).

Fig. 963.—*Fraxinus excelsior.* Vernation of buds showing expanded bud scales and pleated arrangement of young foliage leaves.

Fig. 964.—*Acer pseudoplatanus.* Vernation of bud showing folded young foliage leaves and terminal inflorescence.

Leaf Duration.

The duration of leaves, at least in perennial plants, is usually short compared with the life of the plant which bears them. Deciduous leaves live for only one vegetative season and are then shed in a senescent condition, although still alive. This only takes into account their life as adult leaves, but in many instances they are formed in the bud during the early part of the preceding season and remain enclosed in the bud in an immature state throughout the following winter before developing to maturity, so that they may properly be said to live for two seasons. Even the so-called evergreen leaves have a relatively short lifetime, indeed it may be said that the difference between a deciduous plant and an evergreen is only that the latter never sheds all its leaves together. In many evergreens among the Dicotyledons the leaves last no more than one year, while those which are longest lived endure for not more than five years. Among some of the slow growing Monocotyledons, such as *Agave*, this age is probably exceeded, but details are lacking.

LEAF DIFFERENTIATION.

The development of leaf rudiments from their meristematic primordia at the growing point of the stem is by no means simple and we are still far from a full understanding of the process. Yet the importance of the leaf rudiments, not only morphologically but physiologically, and their dominant part in the development of the shoot can be understood when we realize that these minute meristematic rudiments produce the auxins which both stimulate and inhibit growth in all parts of the shoot.

We have already pointed out that leaves are invariably lateral outgrowths ; to this we may now add that they are invariably outgrowths from meristem tissue and are never adventitious, though, in some exceptional cases, the meristem from which they come may not be that of the stem apex. In some monocotyledonous seedlings, as in the sporelings of some Ferns, the formation of the first few leaves precedes the organization of an apical growing point, while the cotyledons are never, in any case, the product of a stem apex. Indeed the cotyledon of Monocotyledons such as *Iris* is truly terminal. The anomalous cases of leaf origin in *Lemna* and in the Podostemaceae have already been mentioned (p. 828). The extent of the apical meristem which is involved in the formation of a leaf primordium appears to be very variable. Among the known cases the majority seem to originate from the tunica, especially where this is two or more layers deep, but in other cases the corpus certainly takes part as well. The earliest part of the rudiment to appear is that which later forms only the apex of the mature leaf, and in some plants, especially some tropical climbers, this first portion of the rudiment grows precociously to form an elongated point or forerunner in which tissue differentiation, including venation, may precede the appearance of the rest of the lamina, of which, however, it may later become an indistinguishable part.

The earliest growth of the rudiment is strictly apical, but this lasts, with few exceptions, only for a short period. In most Monocotyledons apical growth ceases when the rudiment is less than 0·5 mms. long, and the greatest part of leaf growth is therefore intercalary. In Dicotyledons the end of apical growth is usually somewhat later, when the leaf is several millimetres in length. Certain striking exceptions are known in which the apex retains its embryonic character during the whole period of the development of the leaf, which therefore increases progressively in length, like a Fern leaf, and is indeed usually circinate like the leaves of that group, the growing apex being thus protected by being rolled up within a covering of older, more resistant parts. Such is the case in the long leaves of *Drosophyllum*, which is a close relative of the insectivorous *Drosera*, and it is also true of leaves of some species of *Drosera* (Fig. 965), and of *Utricularia*. Leaves are normally organs of limited growth, but in this latter genus the place and functions of

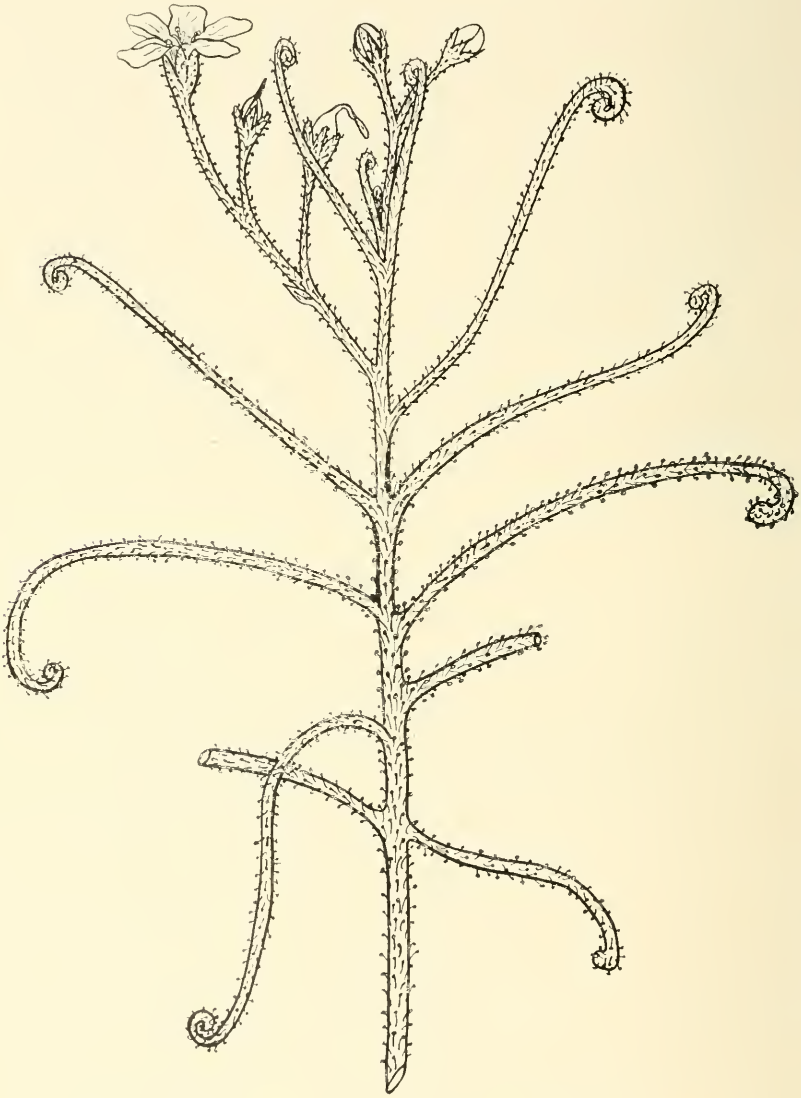

FIG. 965.—*Drosera indica*. Showing apical growth of circinate leaves. (*After Diels.*)

roots, which are absent, are taken over by long thread-like leaves, the rhizophylls, which have a downwardly directed and indefinite apical growth. Only their origin and the occasional occurrence of imperfect insect traps on the rhizophylls remain to show that they have originated from modified leaves and are not, in fact, as in appearance, true roots. In some species of *Utricularia* the persistence of apical growth in the leaves has led to a situation where all distinction of stem, root, and leaf appear to be lost. The vegetative plant consists of creeping axes which may develop either from or into foliage leaves or into rhizophylls with complete promiscuity (Fig. 966). In this connection one may recall that the leaves of *Welwitschia* are also of unlimited growth, though in their case the growth is intercalary.

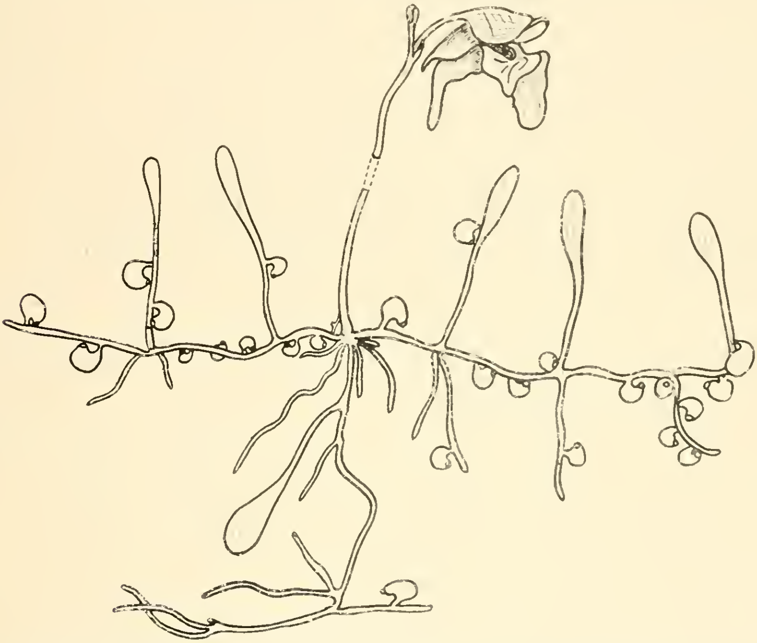

FIG. 966.—*Utricularia coenica.* Flowering shoot showing promiscuous development of branches into either leaves, roots or flowers. (*After Goebel.*)

During the brief period of normal apical growth in the leaf rudiment, the basal portion expands laterally, in accordance with the transverse expansion of the meristem of the stem apex, so that it occupies an increased arc of the circumference of the apical dome. The leaf rudiment in Monocotyledons expands laterally so much that it rapidly encircles the whole growing point like a collar, and the close succession of these collars, each growing actively, quickly pushes the leaf bases of older rudiments centrifugally away from the growing point. This produces the sharp flexure of the leaf-trace strands at the point of their entry into the leaf base, which we have commented upon in the previous chapter, as characteristic of most monocotyledonous stems.

In describing differentiation at the apex of the stem, in Chapter XXI, we pointed out that the procambium usually makes its first appearance in the ring of residual meristem, at separate points in the ring, each point lying at the base of a leaf primordium. These vertical strands of the earliest procambium extend themselves continuously both downwards in the tissue of the internode below and also in an upward and outward direction into the leaf primordium itself. This latter extension is due to the appearance in the primordium, at a very early stage, of a median band of meristem, connecting the end of the procambium advancing from the stem with the apical meristem of the primordium, which is still active in this early phase of development (Fig. 967). The rapid elongation of these meristem cells to form procambium in the leaf is probably the reason for the relatively rapid growth in length which occurs in the young rudiment. This growth in length is accompanied by radial growth in thickness, so that the primordium assumes the form of a slender cone, somewhat flattened on the axial side. This constitutes the petiolar-midrib region of the leaf, which is differentiated before the lamina makes its appearance. The petiole does not, therefore, arise as a structure intercalated between the lamina and the leaf base, as older accounts maintained, but is one of the primary structures of the leaf.

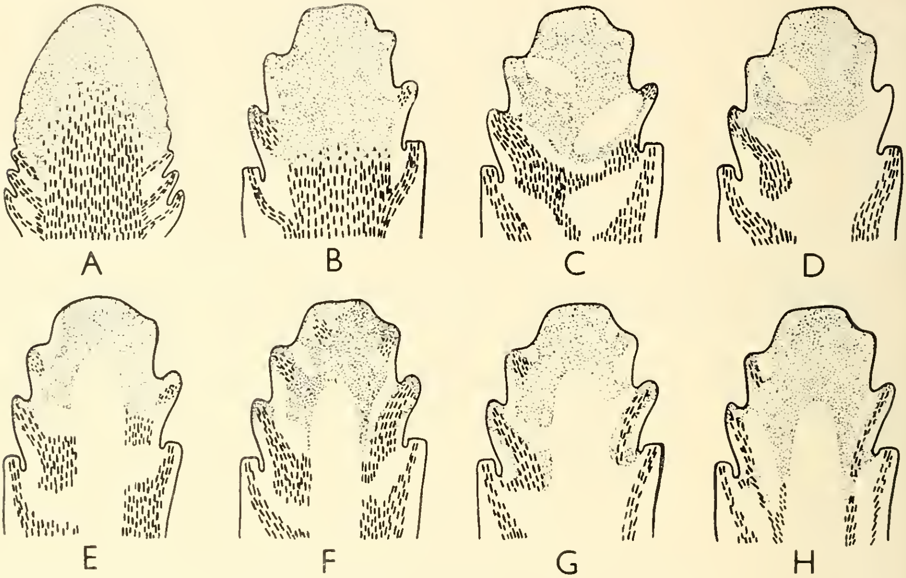

Fig. 967.—Types of relationship between meristem and the procambial supply to the leaf rudiments. A, Microphyllous with protostele. B, Megaphyllous with protostele. C, Polycycly through invasion of stele by leaf gap parenchyma. D, Dictyostele with medulla formed by fusion of leaf gap parenchyma. E, Dictyostele with pith formed endogenously. F, *Osmunda* type. G, Dicotyledonous type. H, Monocotyledonous type. (*After Kaplan.*)

The lamina begins to differentiate from the upper or adaxial portion of this petiolar-midrib structure, in the form of two thin marginal ridges of meristem which appear before the rudiment is as much as 1 mm. long. Very little is known about the early development of compound leaves, but it has been observed that the pinnae arise on the side of the rudimentary rachis as hemispherical cushions, replacing the continuous marginal ridges of meristem which are characteristic of the simple leaf blade. These separate rudiments usually arise in basipetal succession, but cases occur of the opposite succession, and also of double succession from the middle in both directions simultaneously.

The rudimentary lamina consists of five to eight layers of cells and it grows by a marginal meristem. The outer cells of this margin seem to divide chiefly in the anticlinal direction, producing the upper and lower epidermis respectively. By periclinal division, however, they produce a line of submarginal initials and it is from these latter that the internal tissues of the leaf are produced (Fig. 968). The course of differentiation may follow various sequences, which differ in detail, but in most cases there seem to be three primitive cell-layers formed. The upper or adaxial layer produces the palisade, the middle layer forms the veins and part of the spongy layer, while the lower or abaxial layer develops into the lower part of the spongy parenchyma (Fig. 969).

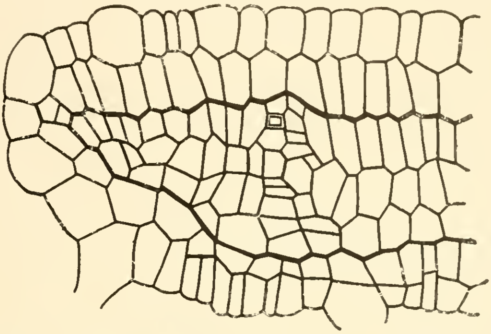

FIG. 968.—*Nicotiana tabacum.* Transverse section of the edge of a young leaf lamina showing genesis of the tissues from marginal and submarginal initial cells respectively. (*After Adriance Foster.*)

Marginal growth ceases as soon as the main outline of the mature leaf has been formed and is succeeded by a protracted period of generalized surface growth, characterized by the predominantly anticlinal division of the cells. The result of this is that the number of layers laid down by the marginal meristem remains practically constant throughout the later development, the only important exception being the formation, by periclinal divisions in the middle layer, of procambium strands from which the veins are developed. The simultaneous longitudinal extension of the veins and superficial growth of the other parts of the lamina, lead to adjustments of position, which are responsible for the characteristic ptyxis or folding of the young leaf within the bud. The final shape of the mature leaf is determined by local variation of growth rates in different parts of the lamina, which may be due to variation in the distribution of auxins in the tissues.

The mature leaf consists of three portions, the **lamina**, the **petiole**, and the leaf base or **phyllopodium**. In most Dicotyledons the leaf base is relatively undeveloped, though it may in some cases give rise to the **pulvinus**, a short cylindrical cushion at the base of the petiole, which acts as a joint between leaf and stem, and by means of which the position of the leaf may be changed. In other cases the phyllopodium gives rise to the stipules (see p. 991). Many Monocotyledons, however, have greatly enlarged leaf bases, forming sheaths surrounding the stem, which may, as in some Grasses and Sedges, be the longest part of the leaf. In Palms with palmate leaves, such as *Chamaerops*, moreover, there is ground for the belief that the petiole also belongs to the phyllopodium, since the ligule, which in the Grasses and Sedges occurs at the top of the sheath, is, in these Palms, at the top of the petiole, immediately below the lamina (Fig. 970).

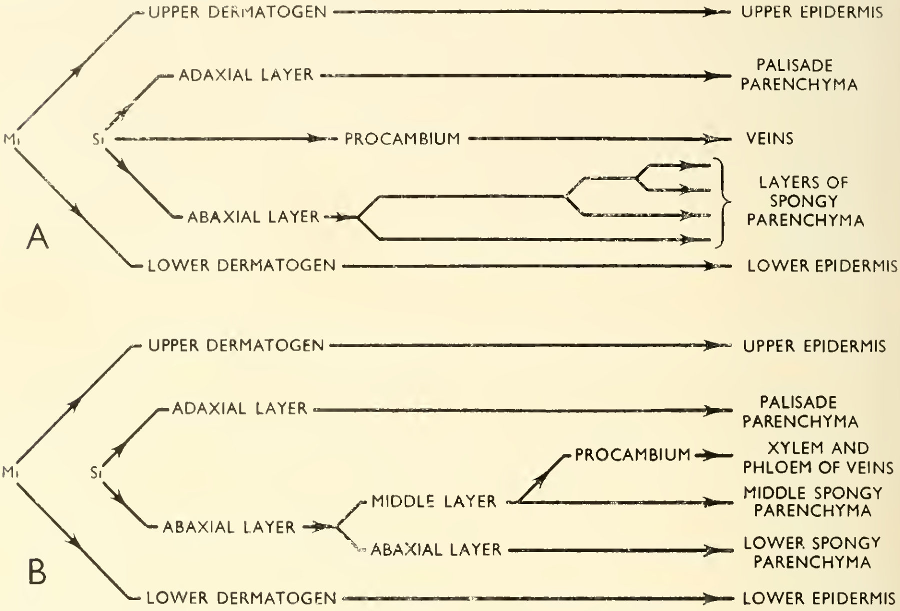

Fig. 969.—Diagram showing two schemes (A and B) of differentiation of the leaf tissues from the marginal initials (Mi) and subepidermal initials (Si) respectively. A, *Bougainvillea spectabilis*. B, *Carya bucklei*. (*After Adriance Foster.*)

These peculiarities are associated with the persistence of intercalary growth in monocotyledonous leaves, which in many instances continue to elongate throughout their life-period by the activity of a basal zone of meristematic cells. An analogous persistence of growth at the base of the lamina in other cases leads to the development of cordate or sagittate leaves with outstanding basal lobes, or in extreme cases to peltate leaves in which there is an extension of the lamina below the point of junction with the petiole, which then appears to be inserted in the middle of the lamina.

The suppression of laminar growth at certain points, which may also occur, gives rise to the irregularities of outline which we have previously mentioned as characteristic of certain species of *Artocarpus* or *Broussonetia*. In some of the Araceae it may affect, not only the margins, but the central parts of the lamina, giving rise to characteristic perforations which are seen in their most striking development in the large leaves of the tropical climbing Aroid, *Monstera deliciosa* (Fig. 971). Patches of meristematic tissue in the leaf rudiments of this plant die and drop out at a very early stage of development and the margins of the lacunae are covered by a secondary epidermis formed from interior cells of the young leaf.

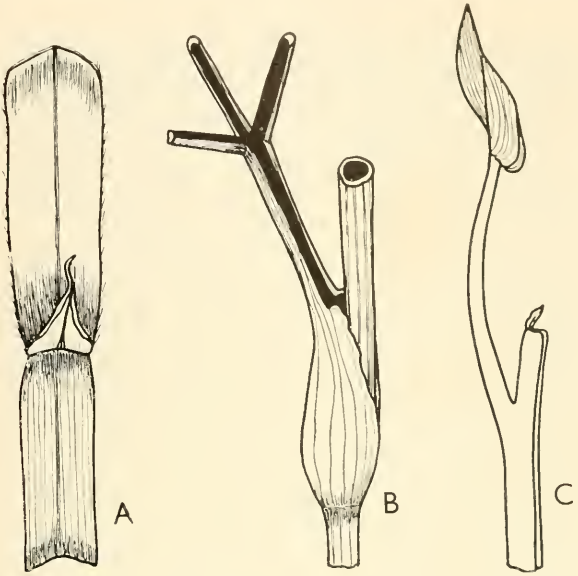

FIG. 970.—Development of the phyllopodium as a leaf sheath. A, *Avena planiculmis*. B, *Heracleum sphondylium*. C, *Pontederia cordata*. The leaf sheath terminates upwards in each case in ligular outgrowths. (A *and* B *after Velenovsky* ; C *after Arber*.)

The early arrest of growth in the midrib, associated with continued growth of the lamina on each side of it may produce either an emarginate leaf such as that of *Liriodendron*, or in extreme cases, an apparent dichotomy of the leaf, which is characteristic of certain genera, such as *Bauhinia*, a leguminous tropical climber (Fig. 972). Leaves of this type may indeed have originated from compound leaves, the arrested growth of the rachis leading to the coalescence of opposite pinnae at their bases, but the principle of development is the same in either case, namely arrest of the principal axis, associated with extended lateral growth. This is not to be confused with true dichotomy of the leaf blade which may sometimes occur as an abnormality, for example in *Salix*.

Palmatifid and pinnatifid leaves may, on the other hand, originate from the opposite type of growth distribution, namely, the greater rate or longer continuance of growth in and close to the main veins, with the result that promontories of leaf tissue are formed, the shape and arrangement of which will depend on the venation.

The cases mentioned above are only a few conspicuous examples of variations in the leaf form which are readily traceable to local variations of growth during the later phases of leaf development, and it is probable that nearly all the normal as well as the abnormal forms of leaves owe their characteristics to similar causes, though direct information on the matter is lacking. Such variations are, however, not entirely due to internal or heritable factors and the environment undoubtedly has a modifying influence. Sinnott and Bailey have pointed out the ecological relationship of certain leaf types to climate, in that certain forms of leaf are predominantly characteristic of certain habitats. For example, leaves or leaflets with entire margins are characteristic of low-lying tropical regions, while leaves or leaflets with non-entire margins are predominant in mesophytic, cold temperate areas, though dry temperate regions usually produce entire margins. The effect of submersion in causing the development of filamentous leaves in aquatics is also well known.

FIG. 971.—*Monstera deliciosa.* Plant showing large perforate leaves. (*Photograph taken in Brazil.*)

The first appearance of primordia at the stem apex is frequently far in advance of the time for their full development, and, after reaching a certain size, a period of dormancy ensues. This is conspicuously the case in the winter buds of trees, which are often formed quite early in the preceding summer. Inside these buds the development of leaf primordia for the next season goes on until the dormant period begins in October or November. When spring comes, the development of this preformed foliage is often surprisingly rapid. In a few cases, such as the Horse Chestnut (*Aesculus*), the whole of the foliage for a given season is prepared beforehand. In others

FIG. 972.—*Bauhinia anguina.* Bifid leaves.
(*After Kerner.*)

the young shoot apex continues to form new leaves for a short time in the early part of the year, but this does not continue much beyond the end of May, after which the apex is again transformed into a winter bud (Fig. 973), in which the later formed primordia are retained till the following spring.

Fig. 973.—*Acer pseudoplatanus.* Longitudinal section of winter bud showing the protective scales and young foliage leaves already formed ready for expansion in the spring. The photograph also shows two smaller axillary buds of similar construction.

PHYLLOTAXIS.

The placing of the leaves on the shoot, known as **phyllotaxis**, is ultimately due to the sequence and the spacing of the leaf rudiments, as they appear on the surface of the meristematic apex of the stem, and it involves some of the subtlest and most obscure of the space-time relationships which we have already indicated as fundamental in apical development. Unfortunately the lack of factual knowledge and the facility with which the subject lends itself to geometrical and mathematical deductions, have combined to lead attention away from the living plant and towards a labyrinth of theory, which has repelled some of the ablest investigators, to say nothing of the great majority of students.

Before entering into any details, there are three main considerations which should be borne in mind, which may be of help in getting a true perspective.

Firstly, the symmetry relationships involved are not peculiar to the arrangement of leaves upon a Higher Plant. Leaves are, as we have tried to emphasize, only a special type of shoot of determinate growth, and the problems involved in their location go far back in evolution, far beyond the evolution of the Higher Plants, indeed beyond the evolution of leaves themselves, and are inherent in every form of branching which depends upon apical growth. It is only in the simplest Thallophyta, with no apical growth, that branching is irregular. As soon as apical growth became an established habit, regularity and rhythm in branch formation became the rule.

The axillary position of the branch initials in Higher Plants tends to obscure this truth, for it seems to make the position of the branches dependent on the position of the leaves. Only in the few examples of non-axillary production of shoots, *e.g.*, in the bractless inflorescences of some Compositae, do we see, and see in such cases with peculiar clarity and beauty, that the same rules of phyllotaxis apply to the arrangement of shoots (in these cases, flowers) which apply to the arrangement of foliage leaves. The conclusion that leaf arrangement is only one expression of a fundamental organic symmetry which rules throughout the plant is strengthened, not only by comparison with the branching of Thallophyta, already referred to, but by the more immediate comparison with the arrangement of vestigial scales, for example on rhizomes, or with the spines of Cacti, which show the same symmetrical order of formation, though remote from foliage leaves in form and function.

Secondly, that the position of a leaf primordium on the stem apex is determined before even the smallest external indication of its growth is visible. It follows that the determining factors, whatever they may be, are internal and protoplasmic and are those factors which control the distribution of growth-potential in the meristem. External factors, therefore, such as contact-pressures against neighbouring primordia, which only come into play after the rudiment has started to grow, cannot be determining factors with regard to its position, however important they become later in influencing its development.

There are many reasons for believing that a leaf is closely identified physiologically with the portion of the axis immediately around and below its point of insertion and that a similar demarcation into leaf fields or primordium fields exists at the apex. Each leaf primordium, appears in the centre of such a field, and its position is predetermined by the mosaic of fields covering the surface of the growing point.

Thirdly, that the geometrical relationships which are exhibited by developing primordia when the dome-shaped surface of the apex is projected on to a plane surface, while beautiful and interesting in themselves, are irrelevant to the question of the origin of the primordia. They do not control the initial spacing of the primordia but follow as necessary consequences of that spacing. That this is so, is illustrated by the frequent irregularities or changes of phyllotaxis which may be observed on one plant or even sometimes on one shoot. If the established symmetry had a predetermining effect on the appearance of new rudiments at the apex such changes should not occur, but in fact they do, and they may even be to some extent experimentally controlled, which serves to show that the origination of new primordia is independent of the pattern which develops as an effect of their arrangement.

A homely parallel may be drawn with the action of a gardener who plants his successive rows of seedlings equidistantly and alternates the positions of plants in successive rows. He might be interested or amused if it were pointed out to him that by so doing he was creating a quincuncial pattern on the ground, but that has no determining effect upon his choice of spacing, which is dictated solely by the wish to give his plants the maximum of light and air. The causation is, so to speak, physiological, the inevitable consequence is a morphological pattern.

A similar confusion of cause and effect is illustrated by the contention that leaf arrangement is dictated by the need to avoid the overshadowing of lower leaves by those higher up ; a good example of teleological argument. Its weakness is easily perceived when we consider that some common types of leaf arrangement, *e.g.*, the decussate type (see below) are not efficient in this respect ; or again that the same arrangement may be shown by the scales on a rhizome and the leaves on the aerial shoots ; or lastly that means exist for subsequent adjustment of the positions of growing leaves, whatever their phyllotaxis, to ensure a leaf mosaic. In other words the avoidance of overcrowding among leaves is an effect, not a cause. That it is a desirable effect in most circumstances is undeniable, and it may well be that natural selection has favoured certain types of phyllotaxis in consequence, but that does not invalidate the argument against it as a true cause of phyllotaxis. The study of phyllotaxis has suffered from the historical accident that it was approached at first from the wrong end, that is to say, from the examination of mature shoots with elongated internodes, while the really critical conditions at the apex were not examined until recently.

On mature shoots there are three fundamental types of leaf arrangement : *i.e.*, in opposite pairs, or in circles called **whorls**, or singly at the nodes. A survey of the families of Angiosperms shows that in certain families one or other of these types may predominate almost exclusively, *e.g.*, opposite pairs of leaves in Labiatae, but it is not possible to say, on the basis of their systematic occurrence, that any one of them appears to be definitely more primitive than the others. Nor is this surprising if we recollect that the establishment of these types must have long antedated the evolution of the Angiosperms. There is some evidence that, in certain families or genera, the arrangement in opposite pairs may have given place to the simple arrangement of leaves singly. We have touched upon this previously in speaking of heterophylly, and there is, additionally, the evidence from seedlings that not only the cotyledons but the first one or two pairs of epicotyledonous leaves are frequently opposite, while the later leaves are formed singly at the nodes. Such conclusions are, however, of strictly limited application.

One of the most general rules of construction in radial axes is that of the equidistance of parts, which holds good not only for outer members but also for internal structures such as vascular bundles. This rule is followed both in the opposite and in the whorled phyllotaxis. Opposite pairs of leaves, moreover, usually alternate at right angles with those above and below them, thus forming four ranks, the **decussate** arrangement. Paired leaves in two ranks only, the **distichous** arrangement, are relatively rare, though single leaves alternating in two ranks are common in Monocotyledons and are almost universal in the great families of the Iridaceae and Orchidaceae.

The opposite and the whorled phyllotaxis are closely similar in that they imply symmetrical, radial growth at the apex with equal spacing of the primordia, and the paired condition may be looked upon as simply a whorl of two members. As both, except for the bilateral distichous cases, imply radial symmetry of growth at the apex, they are commoner in orthotropic than in plagiotropic shoots. A tendency towards the development of bilateral or even dorsiventral symmetry may, however, often be observed in the growth of the axillary buds of such leaves, when the leaves themselves do not show it. For example, all the axillary shoots on one side may be stronger than those on the other side of the axis, or may become flowers while the buds standing opposite develop vegetatively. This produces a secondary dorsiventrality even in an orthotropic shoot and is usually associated with the presence of truly dorsiventral shoots in members of the same family. In other cases, strong and weak shoots may alternate on each side of the main axis, thus showing a tendency towards spiral organization. The close relationships of opposite and whorled arrangements is shown by their tendency to pass one into the other. Individuals can often be found, of species which normally bear opposite paired leaves, with three or even four leaves at each node, or sometimes only at certain nodes. The essential similarity of the two conditions lies in the simultaneous formation of several primordia at the apex, but the number actually formed seems to bear some relation to the vigour, if not the size, of the apex, since it tends to increase as the plant matures. It should be noted that in whorls of several leaves, as in those with only two, the members of each whorl alternate in position with those of the whorls above and below.

The rule of equal spacing applies also in the cases of leaves inserted singly, which are by far the more numerous. If we examine a shoot of this kind we shall see, that if we start from any leaf and trace a line from this to the next leaf above it and so on until we come to a leaf which is exactly above the first, in a vertical line, we shall have traced a spiral round the stem. We shall find, further, that the number of leaves intervening between any two in the same vertical line is constant, and so is also the number of turns of the spiral round the stem in passing from one to the other. This means that successive leaves must be equally spaced around the stem, or in other words, that every leaf is separated from the next by a fixed proportion of the circumference of the stem. This is called the **leaf divergence.** By comparing a number of different plants we find that the characteristic divergences are not all the same, but that the number of different divergences is nevertheless limited, and that certain figures occur again and again. Expressed as fractions of the circumference, the divergences found experimentally can be arranged in order thus : $\frac{1}{2}$, $\frac{1}{3}$, $\frac{2}{5}$, $\frac{3}{8}$, $\frac{5}{13}$, etc., a numerical series called, from its discoverer, the Fibonacci series. This series has the property that the numerator and denominator of each fraction are equal to the respective sums of those of the two preceding fractions. It has the further property that the first term, $\frac{1}{2}$, expresses the maximum divergence, and the second term, $\frac{1}{3}$, expresses the minimum divergence in the series.

The maximum divergence, $\frac{1}{2}$, is not very common. It represents leaves which are arranged, singly, in two rows, on opposite sides of the stem and is specially distinguished as the **alternate** or **distichous** arrangement. We have already mentioned that it is commoner among Monocotyledons than among Dicotyledons, and is especially characteristic of Gramineae, Orchidaceae, and Iridaceae. The second or minimum divergence is likewise restricted in occurence, but it is noteworthy that it predominates in the Cyperaceae, a family closely related to the Gramineae. It is also frequent in the flowers of Monocotyledons but is rare among Dicotyledons. A closer approximation than $\frac{1}{3}$ is very rare among higher plants, but cases of $\frac{1}{4}$ or $\frac{1}{5}$ divergence are known, and they form the first term of another Fibonacci series.

The divergences of $\frac{2}{5}$ and $\frac{3}{8}$ are the commonest among Dicotyledons. Higher fractions are characteristic of shoots with either very narrow or very closely set leaves or branches, like some inflorescences. As the higher fractions of the series are approached, it becomes increasingly difficult to say which leaves are directly above each other, as the number of intervening turns of the spiral increases, approaching the limiting case in which no two leaves are directly superposed, which occurs in some very condensed shoots such as gymnospermic cones in which the fractional denominator approaches infinity.

In describing these spiral arrangements it is customary to refer to the vertical rows of superposed leaves as **orthostichies**. The number of orthostichies present will obviously equal the denominator of the divergence fraction. The mature stem has normally only one spiral of leaves, traced conventionally in the anticlockwise direction round the stem, which represents the sequence in which the initials were produced at the apex and is therefore referred to as the **genetic spiral** (Fig. 974). The existence of this spiral does not, however, imply any twisting of the axis during growth, nor does it imply any spirality or " spiral tendency " as it used to be called, at the apex. It is simply a geometrical figure which is " described " as the mathematicians would say, by the equiangular spacing of the primordia on an elongating axis. As the genetic spiral approaches the apex it becomes more and more condensed towards a flat helix, and the young leaves or primordia approach closer and closer together. The number of orthostichies represents, in each case, the number of primordia which exist simultaneously at any given level of the apex, and must naturally be related to the size of the apex itself. These primordia are not, of course, except in whorled phyllotaxis all *formed* simultaneously. For example in stems with decussate phyllotaxis, although there are four orthostichies, only the primordia of one pair of leaves are formed at the same time. They leave only a small flat apex unoccupied between them and it is not until after an interval or **plastochrone**, during which the apex again grows forward into a dome, that another pair is formed.

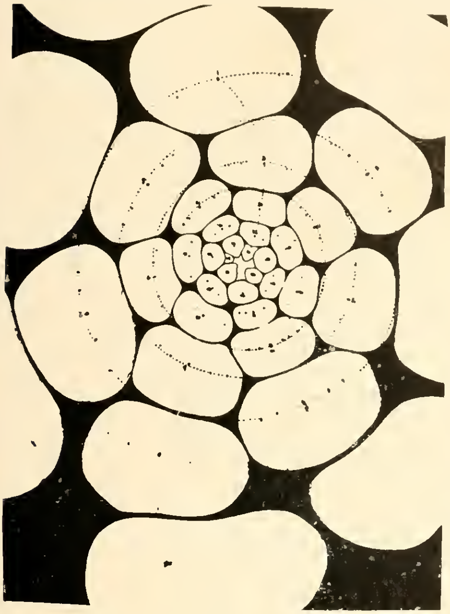

FIG. 974.—*Sedum reflexum.* Transverse section through the stem apex showing the genetic spiral of the leaf rudiments.

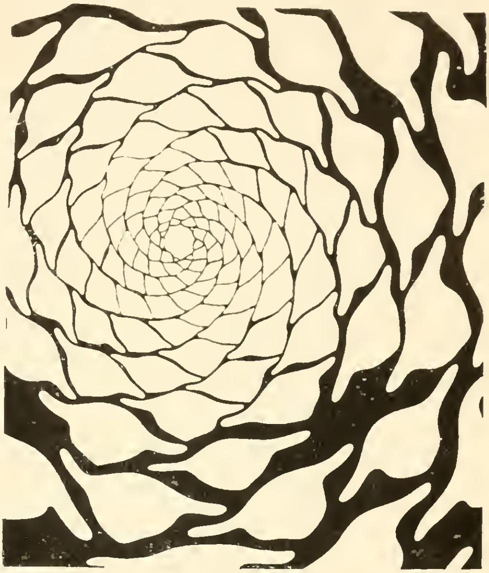

FIG. 975.—*Euphorbia wulfenii.* Transverse section through the apical bud showing the leaf rudiments in parastichies.

(*From Church, "On the Relation of Phyllotaxis to Mechanical Laws," Williams and Norgate, Ltd.*)

As the primordia approach each other towards the apex, secondary spirals become evident in their arrangement. These are called **parastichies** (Fig. 975), and they are purely a geometrical consequence of the packing of the rudiments together. They can be traced both clockwise and anticlockwise. In whorled constructions the number of parastichies in each direction is equal. Spiral phyllotaxis always produces an unequal number.

The mathematical deductions which may be derived from these arrangements, however interesting, leave untouched the primary biological question of why a given rudiment arises at a given point on the apex, since its inception must be determined before it appears. The apex is a dome, the surface of which is undergoing uniform expansion outwards from its apex as centre (Fig. 976). On this growth-field secondary centres are established which become primordia of leaves, and we have still no better account of the phenomenon to offer than that originally proposed by Hofmeister, namely, that each primordium tends to appear in the largest unoccupied space left by its predecessors. This seems to accord not only with observations, but with what we should expect from the conditions of competition for nutriment between primordia, such as must obtain at the apex. It does not exclude the possibility that the whole apex may be physiologically mapped out into primordium fields, *e.g.*, by intersecting gradients, even where it appears to be still undifferentiated ; it simply points to the sequence in which these fields will tend to develop.

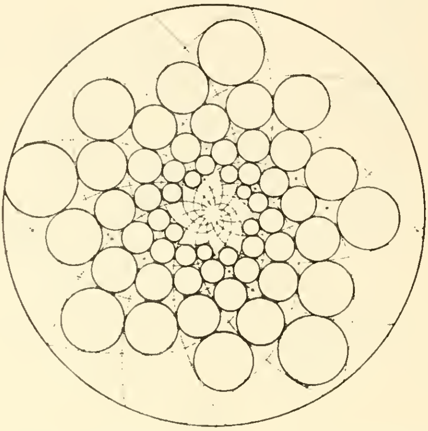

FIG. 976.—Plane projection of an apical dome undergoing uniform centrifugal expansion. The growth fields are outlined by the dotted lines and the positions of successive leaf primordia are represented by circles. (*From Church, "On the Relation of Phyllotaxis to Mechanical Laws," Williams and Norgate, Ltd.*).

ORGANS OF REDUCED FOLIAR TYPE.

Every Higher Plant produces various foliar organs which differ from the foliage leaves and are usually spoken of as " reduced," which does not necessarily imply their evolution from foliage leaves, but merely that in comparison with them they have a lower grade of organization. We shall not deal here with floral leaves, but among vegetative structures we may cite as examples :—

1. CATAPHYLLS : reduced leaves on the lower part of a plant or a shoot, including the cotyledons, the scale leaves on rhizomes, and especially, the bud scales, which mark the base of future shoots.

2. HYPSOPHYLLS : reduced leaves on the upper part of a plant or shoot, especially the **bracts** in the inflorescence region, and including the **prophylls** or **bracteoles** of the individual flowers.

3. STIPULES : foliar appendages attached to the leaf base or the petiole, and including the **stipellae** which are attached to individual leaflets in a compound leaf.

4. LIGULES and other scale-like appendages of certain leaves, such as the **intravaginal scales** in some Monocotyledons.

The morphology of these structures and their relation to foliage leaves is still, in many cases, obscure, but some have been investigated in detail.

Cataphylls are in most cases homologous with leaves, but only in a minority of cases is a scale equivalent to a whole leaf or has a recognizable likeness to the fully developed leaves, though in some examples, *e.g.*, bud scales of *Syringa vulgaris* (Lilac), a series of forms may be traced between the outer typical bud scales and the juvenile leaves within the bud. Another condition is that in which the scale corresponds to the leaf base, and this is probably the commonest case. There is a difference in the rates of development in the upper and lower zones of the scale rudiment, the upper zone, corresponding to the petiole and leaf blade, failing to develop beyond the rudimentary state. In some buds, however, a succession of forms may be found, showing the gradual development of the lamina at the apex of the scale, the proportion of lamina to leaf base increasing towards the centre of the bud until the normal form of the leaf is reached. Such intermediate stages are well shown during the opening of the bud in such woody plants as *Ribes* (Fig. 977) and *Aesculus*.

FIG. 977.—*Ribes sanguineum.* A series showing the continuous transition from the outermost bud scales consisting of leaf base only, to the mature foliage leaves with expanded leaf blades.

The divergence from typical leaf development begins at a very early stage of scale formation. In opposition to the usual idea of reduction is the fact that there is no diminution of growth rate in the development of a bud scale such as that of *Aesculus*. Actually the development of the scale rudiment is faster than that of the leaf. There is more rapid vacuolization and maturation of the cells, but growth is limited to the margin and soon ceases. Scale formation and leaf formation are two distinct periodic phenomena, and are apparently determined by organismal factors, the fate of the rudiment being decided before its appearance, though the resultant structures may finally differ so greatly that it is not possible to homologise their parts.

The cataphylls of the winter bud mark the base of each year's shoot-generation during the growth of a perennial plant. Similarly the base of the first shoot in the seedling frequently bears cataphylls. Following the cotyledons a succession of reduced leaves may be produced, increasing in size at each node and leading eventually to the mature leaf form. Unlike the bud scales these cataphylls are separated by internodes, the length of which increases upwards on the stem.

Cataphylls, like other leaves, usually subtend axillary buds, which are, however, of reduced size and are generally dormant. If they are stimulated to growth, as, for example, by severe pruning, they form dwarf and slow-growing shoots, or spurs, on which flowers are borne.

A third type of scale formation is that from the stipules of leaves. Many buds have scales of this type, for example, *Alnus*, where the bud is covered by three scales, two being the stipules of the outermost leaf and the third being one stipule of the second leaf. Other conspicuous examples are *Magnolia* and *Liriodendron*, in which the stipules fall off when the buds open and their protective function is finished. In the buds of the Oak and Beech there may be a considerable number of such stipular bud scales, each of which is a double structure formed of a pair of stipules, the lamina being reduced to a microscopic point. Only the two outermost scales are simple.

Hypsophylls originally included all the floral leaves, petals and sepals as well as bracts, but the term is now generally limited to the latter. Bracts may be green organs with the same assimilatory capacities as foliage leaves, or they may act as protective coverings to the flower or inflorescence buds (Fig. 978), and in some cases they may be specially coloured and serve the biological end of increasing the conspicuousness of the flowers. If a hypsophyll subtends an axillary structure, this is usually, though not invariably, a flower or a flowering branch and its peculiarities of form seem to be linked with this fact, since in cases where an inflorescence produces fresh vegetative shoots, the normal foliage generally reappears on these. The term **bract** is usually applied to a hypsophyll subtending an inflorescence, and the term **bracteole** to one which subtends a single flower, but the distinction is not universally applied, and the term hypsophyll itself, which merely serves to unite the two categories of organ, is not, therefore, of much general utility.

Like the cataphylls, the hypsophylls are often connected with the normal leaves by intermediate forms which make a sharp line of division impossible, and again like the cataphylls, they may arise in three different ways. Firstly, by a reduction in development of the entire leaf ; secondly, and more commonly, by a reduction or abortion of the lamina and petiole, and a correspondingly enhanced development of the leaf base. This may often be perceived by a comparison of the venation with that of the normal leaf. The leaf base usually has a distinctive venation, different from that of the lamina, even when it is coalescent with it, and this type of venation will be found to correspond to that in the hypsophylls. Thirdly, they may be formed by the modification of stipules in some plants belonging to families such as the Rosaceae, where these latter organs are present.

FIG. 978.—*Phylacium majus.* Inflorescence showing resupinate bracts acting as protective coverings to the flowers. (*After Collet and Hemsley.*)

The term **stipules** has been loosely applied to outgrowths at the base of a leaf of very various forms and natures (Fig. 979). Some of these are, however, not of true stipular character and the name should be limited to paired lateral outgrowths of the leaf base, corresponding to the lateral lobes or leaflets which may be produced from the laminar portion of the leaf. Simple though such a definition may appear, it is by no means easy to apply it in all cases. Fusions and displacements during the process of development may obscure the lateral or the paired nature of stipules, so that opinions differ regarding the interpretation of many structures, such as, for example, the ochrea in the Polygonaceae (see p. 993). We shall here relegate the ligules and intravaginal scales of the Monocotyledons to a separate category, while admitting that this is a disputable opinion.

There is a widespread belief that true lateral stipules are altogether wanting in the Monocotyledons, but Glück has shown that genera in several families, notably *Hydrocharis*, *Potamogeton*, and *Dioscorea* possess free lateral outgrowths of the leaf sheath which must be accepted as stipules.

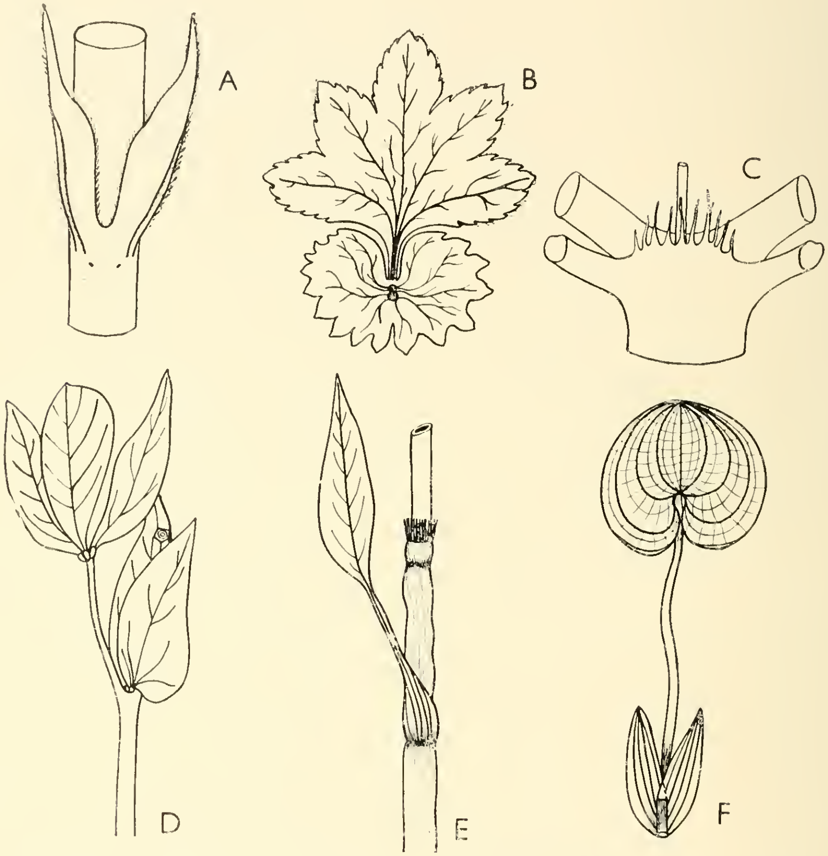

FIG. 979.—Various types of stipules. A, *Boehmeria nivea*; axillary stipules. B, *Alchemilla vulgaris*; antidromous stipules. C, *Euphorbia peplis*; interpetiolar stipules. D, *Lotus corniculatus*; pseudo-stipules. E, *Polygonum hydropiper*; ochrea. F, *Hydrocharis morsus-ranae*; monocotyledonous stipules. (A *to* C *after Gluck*; D *to* F *after Velenovsky*.)

In Dicotyledons examples of **pseudo-stipules** are not uncommon, especially in genera with compound leaves, such as *Cobaea* and *Vicia*, in which the lowest pair of leaflets may develop so close to the leaf base that they simulate stipules and may even envelop the stem. *Pisum* is apparently the reverse case, where true stipules become enlarged until they appear to be the lowermost pair of leaflets.

Pseudo-stipules may arise in a variety of ways other than by modification of basal leaflets. They may, as in *Cestrum* for example, be the paired basal leaves of an axillary shoot. In the simple leaves of *Viburnum opulus*, the leaf base carries a number of paired projections, which are usually tipped with glands and might be taken for true stipules if gradations did not occur between them and the nectary glands further up the petiole. Both sets of structures are modified leaf teeth and belong to the laminar portion of the leaf which runs down the petiole to the base in the form of two parallel ridges. Similar examples may be found in other species. Stipules and pseudo-stipules may both exist together in the same plant, as in *Lotus*, where the foliolar pseudo-stipules cover and hide the glandular stipules.

Plants with opposite leaves often have stipules which are placed *between* the leaf bases and ensheath the young leaves of the next node above. Such interpetiolar stipules are particularly striking in *Galium*, where only two of the apparent leaves at each node are true foliage leaves, the rest, two to eight in number, being stipules which closely resemble the leaves but do not receive trace bundles directly from the stem stele as do the true leaves.

True stipules may often be found united together. When the union is along their inner margins they may form a single organ bridging across the leaf axil. If, on the other hand, they fuse by their outer margins, the united structure may be **antidromous**, that is, apparently opposite to the leaf. Stipules belonging to opposite leaves may also unite to form partial or complete sheaths around the node, as in the Rubiaceae.

The **ochrea**, mentioned before, is a membranous sheath, arising from the leaf base and surrounding the axillary bud and the stem for a short distance above the node. It is a family character in the Polygonaceae, and also occurs in some Ranunculaceae, such as *Caltha*. It has been interpreted as derived from the axillary fusion of two stipules, but it develops as a single sheathing organ, and seems to be better regarded as a tubular upgrowth of the leaf base and not of stipular nature.

Whatever be their morphological origin, stipules and pseudo-stipules definitely function as protections for the leaf rudiment, which they often precede in development, and for the axillary buds. In many cases they are **caducous**, that is, they are shed when the leaf approaches full development, thus showing that their chief importance is then past, but in others they are retained, and, by carrying on photosynthesis, they contribute something, though in most cases probably not much, to the nutrition of the plant.

Three types of leaf structure remain to be mentioned. The first are called **intravaginal scales** because they appear in the axil within the leaf sheath or vagina of certain Monocotyledons, especially members of the Helobiae. They take the form of small tooth-like scales, generally linear or lanceolate, and they actively secrete mucilage (Fig. 980). They are not stipules, since they may occur in association with stipules or even, as in *Hydrocharis*, in their axils, and they are generally regarded as trichomes. They may be single or serial, and according to Arber they arise either from the surface of the axis or from the dorsal tissues of the base of the leaf immediately above them.

Secondly, the leaf base may be enlarged into a wide sheath, or **vagina**, more or less encasing the stem (see Fig. 970, p. 979). This is commonest in Monocotyledons, but is also characteristic of certain dicotyledonous families, notably the Umbelliferae. In many Monocotyledons the vegetative stem remains very short, and a large part of what appears to be the leafy axis is really a cylinder formed by the tightly wrapped leaf sheaths of successive leaves, up through the middle of which eventually grows the flowering axis. This structure is familiar in many Grasses and Sedges but reaches its greatest development in the Banana, where it attains tree-like proportions.

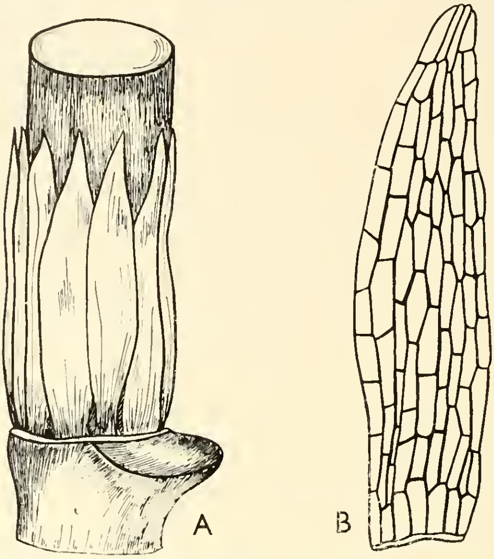

FIG. 980.—*Potamogeton perfoliatus.* Intravaginal scales. (*After Ascherson.*)

Eichler distinguished leaf sheaths which were composed of stipules more or less adnate to the leaf base from those in which the sheath was a simple expansion of the petiole or leaf base itself. Most leaf sheaths in Dicotyledons are of the former nature ; only in a few families, such as the Compositae, where no stipules exist, is the leaf sheath indubitably petiolar. The Monocotyledons rarely possess free stipules, but in them the leaf sheath, which is almost universal, is probably also the product of fused stipules, united to the leaf base. In both groups of Angiosperms the tips of fused stipules may remain free, appearing as a scale at the top of the sheath, known as the **ligule**, which often shows, by its division into two lobes, an indication of its double nature. Indeed, it has been pointed out that ligule and sheath bear an inverse relationship to each other and that the shorter the sheath is, the larger and more stipule-like is the ligule (*e.g.*, in *Trifolium*).

Thirdly, when the laminar portion of a leaf rudiment is suppressed during its development, and the resulting mature structure assumes the appearance and assimilatory function of a leaf, although actually incomplete, it is called a **phyllode**. True phyllodes are not as numerous as they may appear to be on a superficial survey of Angiosperms. The name has been freely applied to cases where the developmental history is unknown and some of these at least have proved, on close investigation, to be true laminate leaves. A well-known case in point is the leaf of certain American species of the umbelliferous genus *Eryngium*, (*e.g.*, *E. agavifolium*), which are linear and have parallel venation (see Fig. 946, p. 959). The suggestion that here the leaf consists of a base and a broadened petiole only is not borne out by the ontogeny, which shows that the lamina becomes long and narrow, and that its pinnae are reduced to long teeth on the leaf margin. There is good reason to believe that the same is true of a number of other apparently phyllodic leaves.

FIG. 981.—*Acacia sp.* Shoot showing phyllodes.

Genuine phyllodes, in which the biological function and the dorsiventral structure of the lamina have been taken over by the petiole or by the leaf base, or a combination of the two, are best known in species of *Acacia* (Fig. 981). Many species of this genus have the multipinnate, compound leaves which are so frequent among the Leguminosae, but certain species, such as *A. longifolia* and *A. glaucescens*, bear only phyllodes which are simple and mostly somewhat leathery in texture. Their venation is reticulate, like that of a typical dicotyledonous lamina, but one peculiarity marks all these phyllodes, namely, the presence of a strong marginal vein, which runs all round the phyllode (Fig. 982). In most phyllodic Acacias, and in the similar structures in species of *Oxalis*, such as *O. ruscifolia*, the seedlings show a striking "recapitulation," that is to say, a series of developmental stages connecting the pinnate leaf type with the phyllodic type (Fig. 983). The first leaves are normally pinnate, with narrow petioles, but in subsequent leaves the petiole is broadened and the pinnate lamina is reduced until a stage is reached at which the petiole has assumed the mature phyllodic structure and the lamina has disappeared or survives only as a small pointed tip to the phyllode.

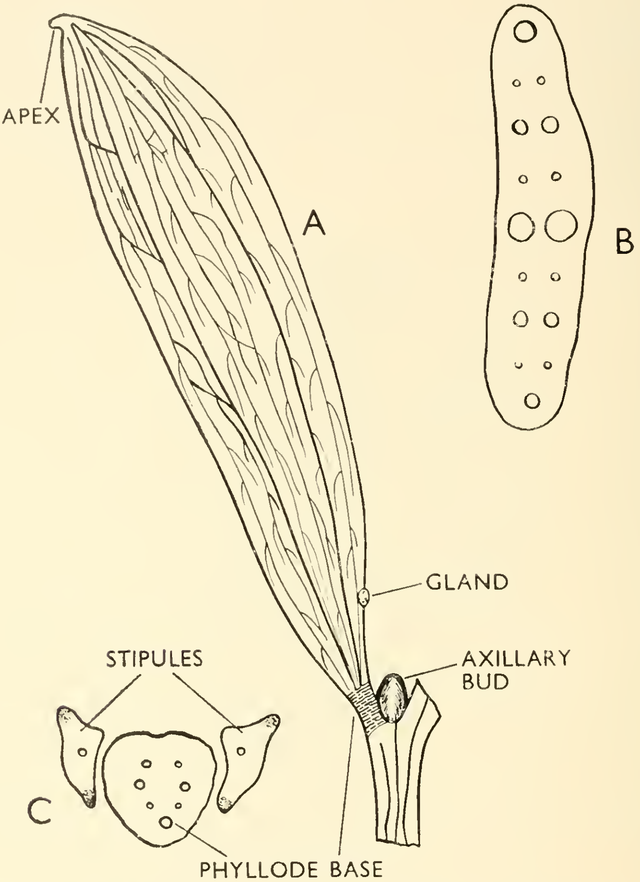

Fig. 982.—*Acacia sp.* A, Diagram of structure of phyllode. B, Transverse section of flat portion of phyllode showing the double row of vascular bundles. C, Transverse section of phyllode base showing stipules and petiolar structure. (*After Boke.*)

The phyllodes of *Oxalis* differ from those of *Acacia* only in that the former are horizontally flattened while the latter are usually flattened vertically.

Phyllodes, like most leaves, arise almost entirely in the tunica of the apical stem meristem. At an early stage in the development of the rudiment a superficial meristem appears over the adaxial surface, which is responsible for the broadening of the structure. At the top of the phyllode is a minute point which represents a rudimentary terminal leaflet, while at its base two stipules are formed. The developmental history, therefore, supports the view that the phyllode is simply a broadened petiole.

FIG. 983.—*Oxalis bilimbi.* Young plant showing transition from ternate leaves to phyllodes.

A. P. de Candolle in 1827 raised the question whether the linear outline and parallel venation which distinguishes so markedly the leaves of Monocotyledons might not be due to their phyllodic nature. This view has been strongly upheld by Arber, who bases much of her argument on anatomical grounds, especially the widespread occurrence of vascular bundles with inverted orientation on the adaxial face of the "leaf." The broadened lamina which occurs in many Monocotyledons (*e.g.*, *Alisma*, *Arum*, *Tamus*, etc.), she interprets as due to a secondary expansion of the apex of the petiolar phyllode, and she further comments that the prevalence among such cases of simple lanceolate or cordate shapes indicates an origin distinct from that of the multiform laminae of Dicotyledons. Even among the Monocotyledons which have leaves with a lamina and a petiole, *e.g.*, the Araceae, the phyllodic tendency shows itself in the frequent lateral expansion of the petiole, associated with the diminution of the lamina, so that the leaf blade is formed of two portions, one above the other, which may be either separate or more or less confluent. There can be little doubt that the leaves of many Monocotyledons are rightly to be classed as phyllodes, but it is perhaps unwise to extend the theory too far, still more to elevate it into a morphological dogma.

A comparison of phyllodes with cataphylls is obvious and it would be difficult to draw a clear line between them. Cataphylls generally consist of a leaf base only, and in phyllodes the petiole is usually, though by no means always involved. The term phyllode is, however, by usage, restricted to organs which carry out photosynthetic functions or replace normal leaves in other ways, for instance, as spines ; while cataphylls are, as we have pointed out above, periodic structures limited to certain growth phases of the plant.

The presence of flower buds on true leaves, as distinct from cladodes, is, at first sight, a puzzling phenomenon from the morphological standpoint. The best-known example is in *Helwingia ruscifolia*, a plant often cultivated in greenhouses. A cyme of small flowers appears from the midrib about half-way up on the adaxial leaf surface. A study of the development shows, however, that the flowers originate from the lower of two axillary buds, the upper one of which remains as a normal axillary bud, while the lower one, the flowering bud, coalesces with the young leaf and is carried outwards by it during its development (Fig. 984).

FIG. 984.—*Helwingia ruscifolia*. Leaves bearing flower buds on the midribs.

In one very peculiar case, *Erythrochiton* (Rutaceae), it is the upper bud which is the flowering one and it coalesces with the leaf rudiment above it, so that the flowers appear on the lower side of the leaf above the node to which they properly belong.

This coalescence of axillary shoots with their subtending leaves is no uncommon occurrence and in the Solanaceae, for example, it often gives rise to striking departures from the normal relationships of leaf and shoot.

SUMMARY OF ELEMENTARY ANATOMY.

The flat blade or lamina of a dicotyledonous leaf is typically a dorsiventral structure, the upper or **adaxial** face differing from the lower or **abaxial** face. Among Monocotyledons on the other hand, dorsiventrality is confined to types with horizontal leaves, those which are borne vertically being often **bifacial**, *i.e.*, with both sides alike, or they may be round, triangular or square in section, without distinction of upper and lower sides, when they are called **unifacial** (Fig. 1011).

There is an upper and a lower **epidermis**, both composed of somewhat flattened cells and covered with a **cuticle**, which varies greatly in thickness, and may be itself covered by a waxy incrustation. The epidermis of both surfaces frequently bears trichomes in the form of hairs or secretory glands. In the epidermis are the **stomata**, which are normally confined to the lower surface, but which may be found on both surfaces in a minority of Dicotyledons and very frequently in Monocotyledons.

Each stoma consists of a pair of more or less curved **guard cells**, whose upper and lower walls are thickened. The guard cells enclose between them a slit-like opening, called the **stomatal pore**, which communicates with the intercellular spaces of the leaf. The guard cells are distinguished from the other epidermal cells by possessing chloroplasts. In certain families there are also **subsidiary** or **auxiliary cells**, which differ from the other epidermal cells by their smaller size and sometimes by their shape. There may be only two of these, one adjacent to each guard cell, or there may be a group of four or more surrounding the stoma (Fig. 985).

The guard cells show characteristic variations of turgor, often with a day and night rhythm. Increased turgor increases their curvature and this widens the pore between them, and vice versa. When they become flaccid the pore is closed, which usually occurs at night. The variations of turgor may be osmotic, due to increased sugar concentration in their sap, and in this connection it should be remembered that the presence of chloroplasts implies the power of photosynthesizing sugars. There is evidence, however, for another view, that the swelling of the guard cells is due to an increased imbibitional power of their contents, conditioned by a rise of acidity in the sap. The physiology of the movement is not yet fully understood.

The stomata are exceedingly numerous, 100 to 200 per sq. mm. being not uncommon, but the number is very variable, not only between plants growing under different conditions, but between younger and older leaves of the same plant, and even in different parts of the same leaf. The latter variation is probably due to differences in the growth rate of particular areas of the leaf during its development, which we have described in an earlier part of this chapter. In Dicotyledons the stomata are scattered irregularly over the surface, but in Monocotyledons they usually form longitudinal rows.

Between the upper and lower epidermis lies the tissue called collectively the **mesophyll**. It is not normally homogeneous but is differentiated into two layers. The upper layer is formed of cylindrical cells lying closely together, with their long axes perpendicular to the leaf surface. This is called the **palisade layer**, from its fancied resemblance to a row of fence slats (Fig. 986). Its cells are rich in chloroplasts which form a practically continuous layer on the long walls. Between the cells are narrow intercellular passages.

Fig. 985.—*Sedum spathifolium*. Epidermal section of the leaf from the lower surface showing stomata with subsidiary cells.

The lower portion of the mesophyll consists of very irregularly shaped cells which are only in contact at their protuberances and among which, therefore, there is a continuous system of large intercellular spaces. This is given the apt name of the **lacunar** or **spongy mesophyll**. Its cells also contain chloroplasts, but not usually so many as in the palisade layer. The distinction of these two layers is clearest in Dicotyledons and is often lost in Monocotyledons, where the whole mesophyll may be spongy.

At the level where the two mesophylls are in contact lie the vascular bundles or veins of the leaf (Fig. 987), varying in size between the massive midrib, which may show some secondary thickening, down to single tracheids at the extremities of the smallest veins. They are normally orientated with their xylem towards the upper surface of the leaf. In Dicotyledons they are often surrounded by a layer of non-chlorophyllous cells, rich in sugars, called the **bundle sheath**.

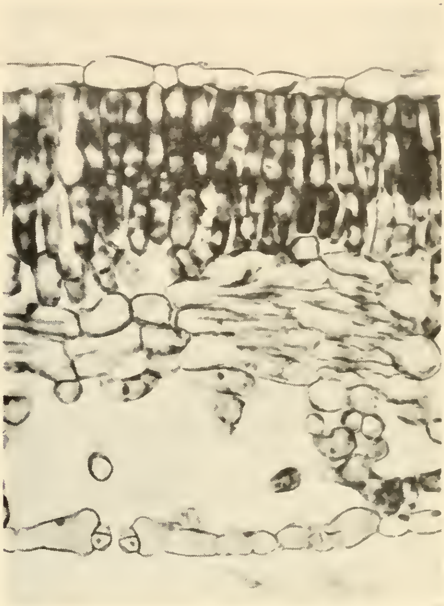

FIG. 986.—*Pyrus malus* (Apple). Transverse section of leaf showing a double palisade layer, spongy tissue and an open stoma in the lower epidermis.

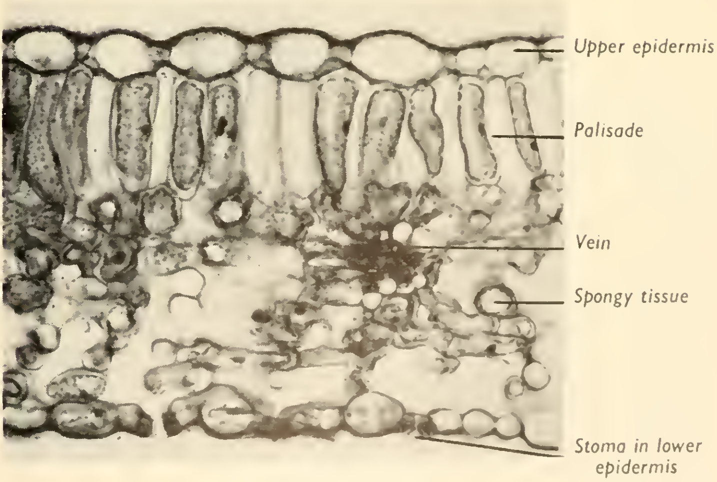

FIG. 987.—*Buxus sempervirens* (Box). Transverse section of leaf showing the position of the veins in the median plane of the leaf.

The leaves of Monocotyledons differ from those of Dicotyledons in having, in general, a lower degree of differentiation in the mesophyll. The palisade layer is seldom well marked and the whole of the mesophyll tissue may be spongy or parenchymatous in character. The veins are parallel and each vein is frequently flanked, above and below, by masses of sclerenchyma, thus forming a rib across the mesophyll, and dividing it into a series of isolated strips between the veins (Fig. 988). As the leaves are usually held vertically the two sides of the leaf tend to be similar in structure, *i.e.*, **bifacial**, with stomata equally numerous on both faces (Fig. 989).

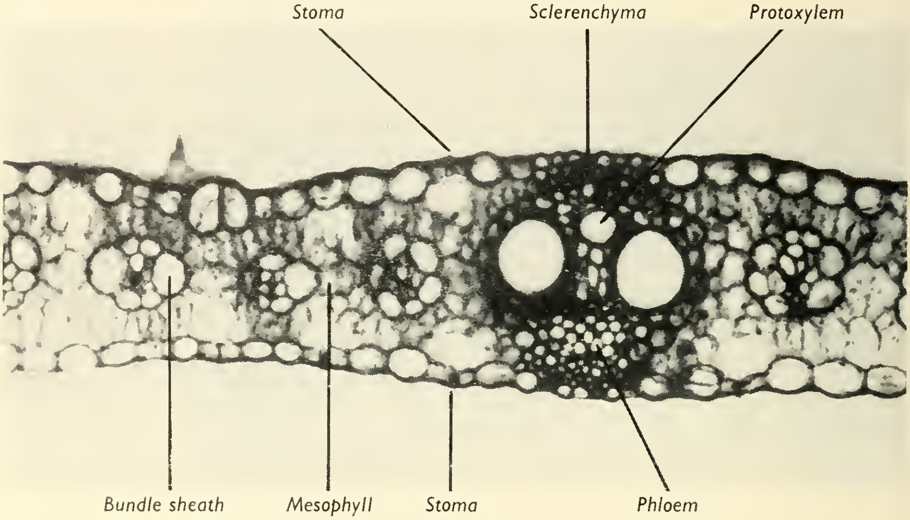

FIG. 988.—*Zea mais.* Transverse section of leaf.

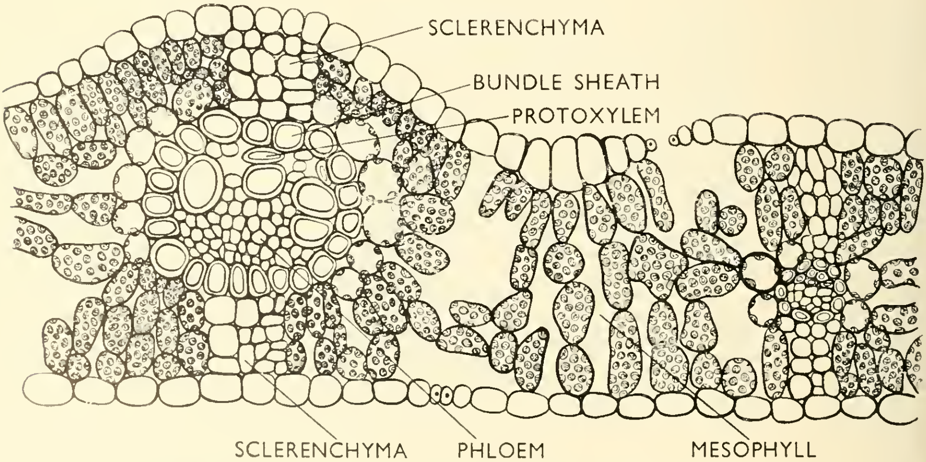

FIG. 989.—*Triticum vulgare.* Transverse section of the leaf showing bifacial structure. (*After Bruner and Weaver.*)

ANATOMY OF THE LEAF.

1. *The Epidermis.*—The epidermal cells of leaves are very frequently **tabular**, that is to say, they are flattened in the anticlinal direction and are broader than they are deep. A characteristic feature is likewise their wavy or undulatory outline, in surface view, especially in the Dicotyledons. In soft-leaved Monocotyledons the epidermal cells are generally elongated, with practically straight walls, but in a few families with hard leaves, such as Gramineae and Cyperaceae, the waviness of the outline reaches an extremity of complexity, resembling the suturing between the bony plates of the skull (Fig. 990). Waviness is usually more pronounced in sun leaves than in shade leaves, even in plants of the same species, and it has been attributed to the progressive hardening of the cuticle from the middle of the cell surface outwards to the margin, its consistency becoming uniform only at maturity, when stretching stops. The increase of the cell-diameter by the stretching of the radial walls will naturally stop first at the points where the hardening first reaches the margins, while other parts of the wall will continue to expand. This view is supported by the fact that waviness affects only the outer contours of the cells, that is to say, on the cuticularized surface. It is not shown by the inner edges of the radial walls, where they meet the inner tangential walls. The degree of waviness is related to ecological conditions, being usually less in plants of dry situations and vice versa. This is probably related to the extent of leaf growth, which is greater in moist conditions.

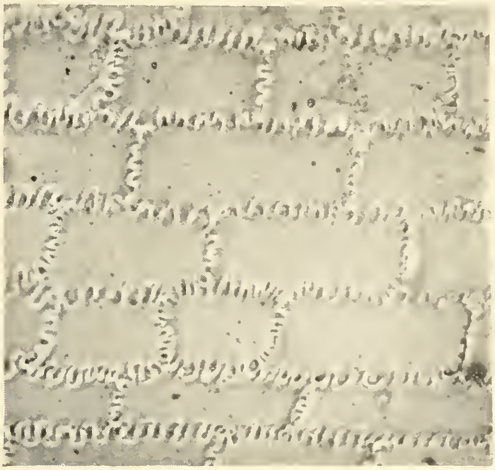

FIG. 990.—*Carex pendula.* Superficial view of epidermal cells of the leaf showing suturing of the walls.

It is quite exceptional to find chloroplasts or, as a natural consequence, starch grains in the epidermis. Instances to the contrary may, however, be found among plants which habitually grow in deep shade and among submerged aquatics, where the epidermis has largely lost its protective functions.

The foliar epidermis resembles that of the stem in being covered with a continuous layer of **cuticle** of varying thickness. This is usually sharply marked off from the individual cell walls below it. The latter are composed of an inner cellulose layer, and between this and the cuticle there is interposed a variable thickness of cutinized wall, consisting of a mixture of cutin and cellulose. This layer may sometimes be absent, even in highly thickened cells. The thickness of the outer wall is not, therefore, a reliable index of its impermeability to water, since the intensity as well as the amount of cutinization may vary considerably. Nevertheless it is generally true that more exposed surfaces have a thicker cutinization than those less exposed, and it follows that the upper surfaces of dorsiventral leaves have usually a thicker coating than the lower surfaces, sometimes twice as thick. Compared with the amount of water vapour which escapes through the stomata, the loss of water through the cuticle is extremely small. Haberlandt showed by experiment that the loss of water attributable to evaporation through the cuticle itself varied between 0·23 (*Aesculus*) and 0·006 (*Hedera*) of the evaporation from an equivalent free water surface.

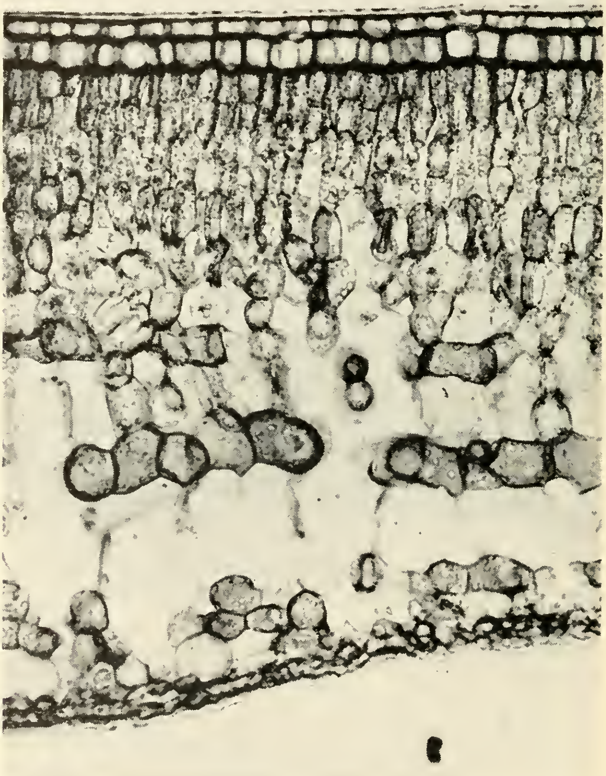

FIG. 991.—*Rhododendron ponticum.* Transverse section of leaf showing multiple palisade and double epidermis with thick cuticle. A xeromorphic type of leaf.

The protective capacity of the cuticle is sometimes enhanced by a coating of wax, which produces the greyish film called popularly "bloom" and known botanically as a **glaucous** surface. This waxy covering is independent of the cuticle and is apparently excreted through it from the living cells. It commonly consists of very minute grains, loosely adherent to the cuticle, but in some Grasses and related plants it takes the form of slender rods attached to the surface by their ends. A third type of waxy covering, in a continuous sheet, occurs especially in Palms. The Wax Palm, *Ceroxylon andicolum*, produces a layer nearly 5 mm. thick, which is scraped off and used to make candles, a single tree frequently producing as much as 25 lb. of somewhat resinous wax. These waxy coverings are of considerable value as a protection against evaporation, not only as an addition to the cuticular covering but also by building up protective ridges round the stomata. In many cases the covering, if rubbed off, can be regenerated.

The outer surfaces of epidermal cells are usually more or less convex, and in many plants they are markedly domed or even conical. The latter type of extension of the cell, when well developed, produces a velvety surface, which is of common occurrence among tropical jungle plants. An ecological advantage has been attributed to this type of surface, in that water falling on the leaf tends to spread by capillarity and hence to dry more quickly, thus offering less encouragement to the growth of epiphyllous Lichens and Bryophyta. The idea, though often quoted as an example of adaptation, rests only on supposition and should not be accepted uncritically.

The epidermis of the leaf bears trichomes of the same types as those borne by the epidermis of the stem, though often in greater abundance, especially on the lower surface. When only a few scattered hairs are present the leaf surface may be described as **hispid** (Fig. 992), whereas a closer covering is spoken of as **tomentose** or **lanate** (Fig. 993). Such densely woolly coats as are implied by these latter terms may be influential in reducing evaporation from the stomatal openings and they are, in fact, commonest in species which habitually grow in exposed places and dry soils, but it must not be inferred that they are confined to such plants or that all plants with a woolly covering stand in need of such additional protection. Only direct experimental evidence can justify such a conclusion. What experience in cultivation does bear out is that woolly plants are usually intolerant of prolonged damp, especially in winter. The thick hairy covering holds moisture tenaciously and probably facilitates fungal and bacterial attack on the tissues.

A number of plants, such as *Platanus orientalis*, *Tussilago farfara*, and *Verbascum olympicum*, have only temporary coverings of hairs on the young leaves, the hairs later disarticulating at their bases, sometimes at a point marked by a specially thin zone of the cell wall, and fall off or are rubbed off, leaving the mature leaf surface bare. Some other types of hairs are shown in Figs. 994, 995 and 996.

The mechanical strength of the epidermis may be very serviceable in preventing the tearing of the lamina, and this is generally due to the cuticle, which not only forms a continuous sheet binding the individual cells together,

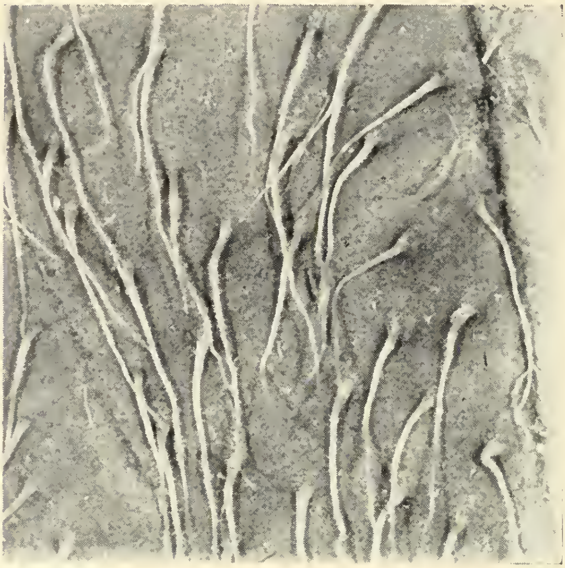

FIG. 992.—*Gossypium herbaceum.* Hispid leaf surface.

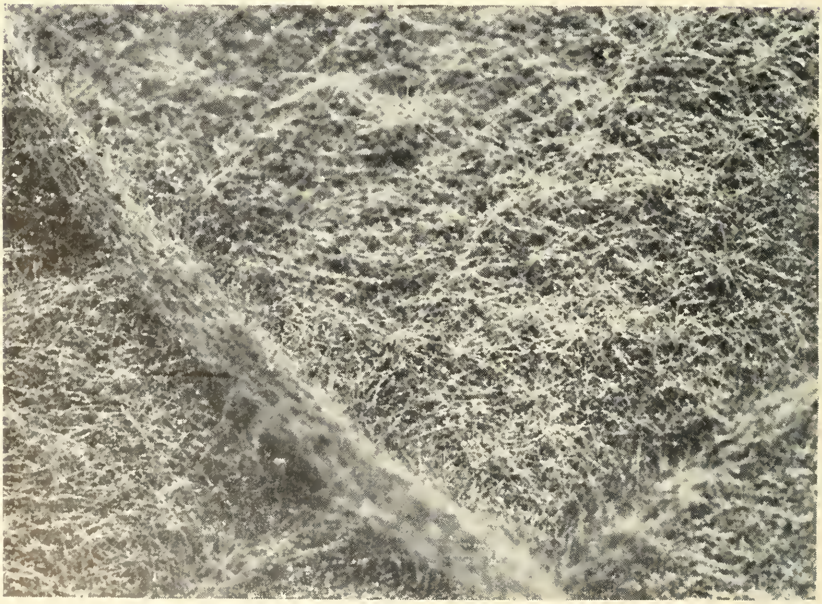

FIG. 993.—*Buddleia variabilis.* Tomentose leaf surface.

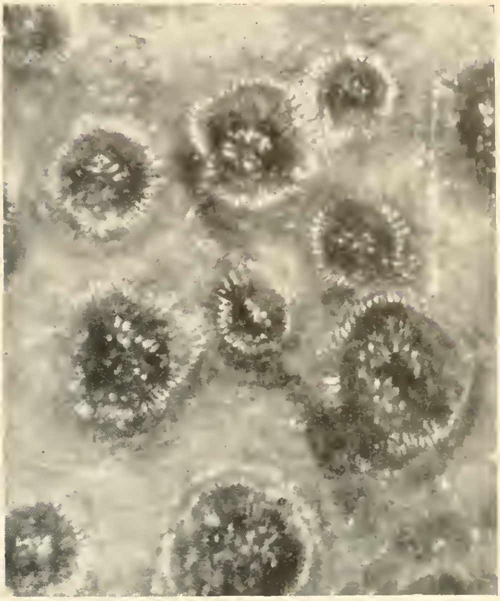

FIG. 994.—*Rhododendron ferrugineum.* Lower surface of leaf showing overlapping peltate hairs.

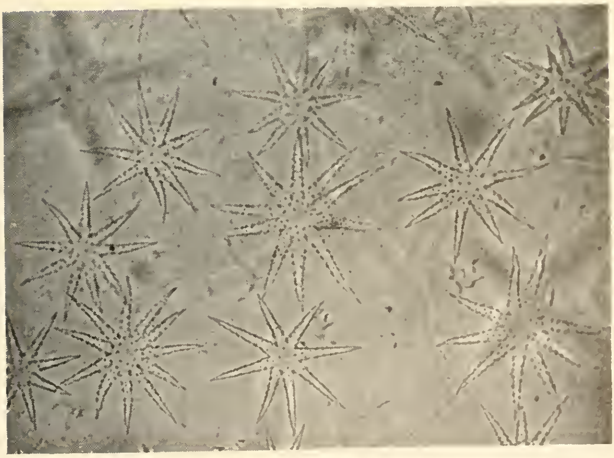

FIG. 995.—*Arabis albida.* Lower surface of leaf with stellate hairs.

but may often be additionally attached to the epidermis by wedge-like processes extending inwards between the cells. The thickening of the epidermal walls is always most prominent at the leaf margins, which are obviously the parts most vulnerable to tearing, and here the epidermis may also be supported by collenchyma or sclerenchyma.

Many species have, however, outer epidermal walls which are calcified or silicified, more commonly the latter. Silicification of the epidermis is particularly strong in Gramineae and in Cyperaceae, as well as in certain Cryptogams such as *Equisetum*, and a rash attempt to tear such plants out of the ground may lead to badly cut fingers from the splintered edges of the siliceous covering.

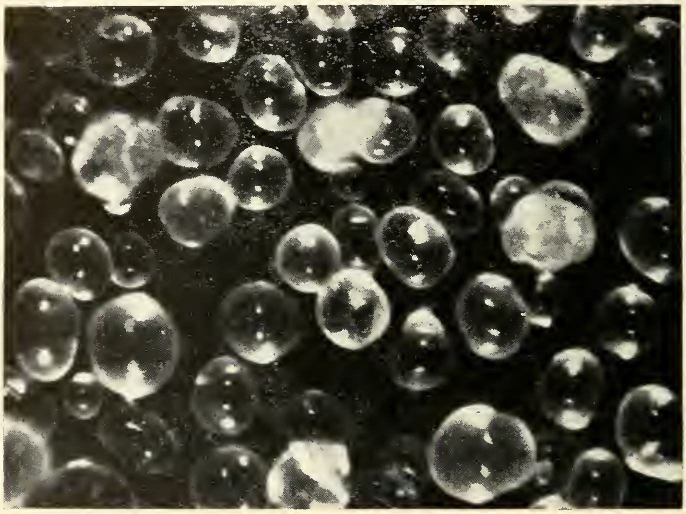

FIG. 996.—*Atriplex hastata.* Vesicular hairs from the surface of a young leaf.

Thickening of the outer epidermal walls is often greater in the middle than at the sides of the cells and there may be a definite papilla, centrally placed, or a lens-like thickening in the substance of the wall itself. Such local thickening, combined with the usually domed shape of the wall, gives the epidermal cells the character of condensing lenses, and Haberlandt drew attention to their probable importance in the perception by the leaf of the direction of the incident light, and hence in the adjustment of the position of the leaf with regard to it. He showed that parallel rays of light falling on the upper epidermis of the leaf, are, in many species, condensed to a bright spot (Fig. 997) on the inner cell surface, and that in at least a few cases it was exactly focussed on this inner surface, so that an image of surrounding objects is formed in each cell, in a manner recalling the multiple eyes of insects. He very justly points out that there is no likelihood of any perception of such images by the protoplasmic lining of the cell, and that the operation of the mechanism depends solely on the difference in brightness between the focused spot of light and the rest of the cell surface. When the leaf surface is in the stable diaphototropic position, *i.e.*, normal to the direction of the sun's rays, this spot is central, but it shifts laterally with any movement of the leaf or of the sun, thus disturbing the equilibrium and providing a stimulus which is supposed to result in phototropic adjustment of the leaf. This hypothesis is supported by observations that if phototropic leaves are plunged in water or if their upper surfaces are painted with liquid paraffin, thus altering the conditions of refraction at the leaf surface, the phototropic reaction is apparently abolished. It is possible, however, that this may be due to the disturbance of some other condition in the leaf, and the hypothesis, though very interesting, cannot be regarded as proven.

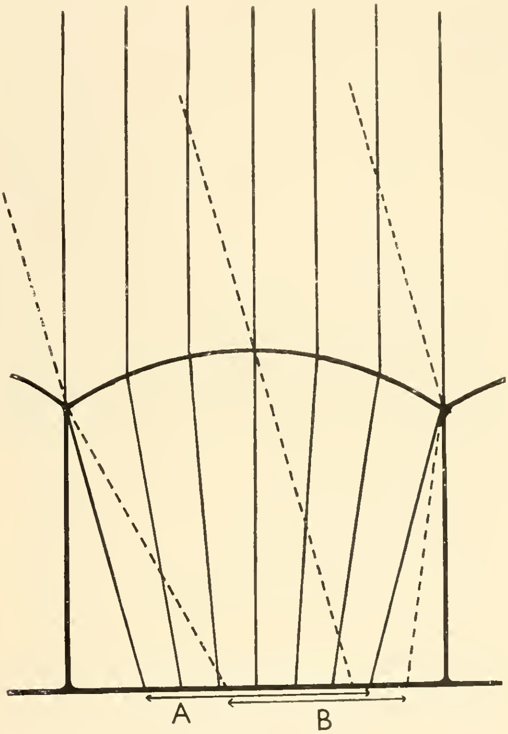

Fig. 997.—Diagram to show the refraction of light rays by the curved outer wall of an epidermal cell. A shows position of the light focus with vertical lighting. B shows the lateral shift of the focus with oblique lighting. (*After Haberlandt.*)

In a few cases, specially enlarged cells of the epidermis with papillate outer walls, are seemingly the organs of this light perception. These have been called **ocelli**, a name borrowed from Zoology. Particularly good examples occur in *Lithops* (*Mesembryanthemum*) *pseudotruncatella*, a small South African succulent (Fig. 998), on the leaves of which the ocelli appear as minute dark spots, due to the greater size and depth of the ocellar cells (Fig. 999).

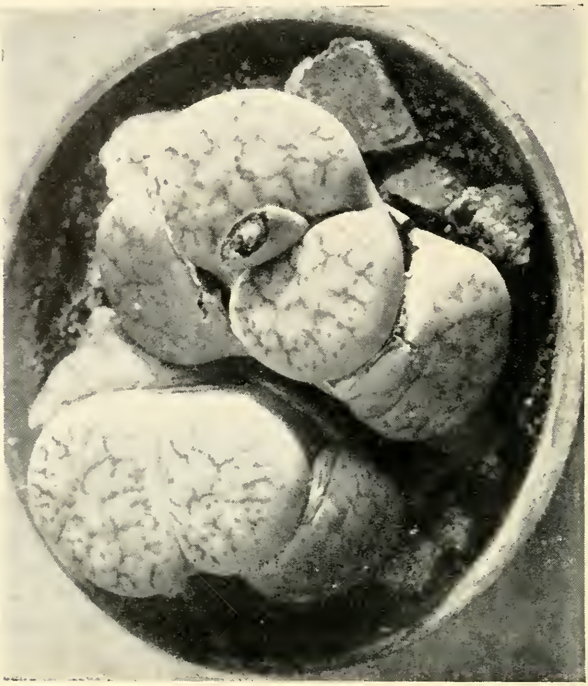

FIG. 998.—*Lithops pseudotruncatella.* Plant showing ocelli as dark spots on the succulent leaves.

A function of the epidermis which must not be overlooked is that of water storage. The amount stored is not normally large, and it would not suffice to supply for long the quantities which are lost by stomatal transpiration, but under conditions of wilting, when the stomata are closed, the epidermis is the first line of defence against cuticular transpiration, and it can be observed that in wilting leaves the epidermal cells shrink and collapse from water loss before the mesophyll cells are affected. As the radial walls of the epidermal cells are usually thin and are in any case covered with numerous pit areas, it is possible for water to move laterally in the epidermis without much difficulty, and water may in this way be supplied to specially exposed spots on the leaf without diminishing the water content of the photosynthetic cells. A case where this may be important is that of undergrowth plants in tropical forests, subjected to the passage of sun flecks which produce for short periods a marked local heating and drying of the air in contact with the leaf.

THE STOMATA.

Although the stomata are a part of the epidermal structure they deserve special description, not only for their intrinsic importance, but also because they are not physiologically a part of the protective system which is formed by the rest of the epidermis. They are the portals of gaseous exchange between

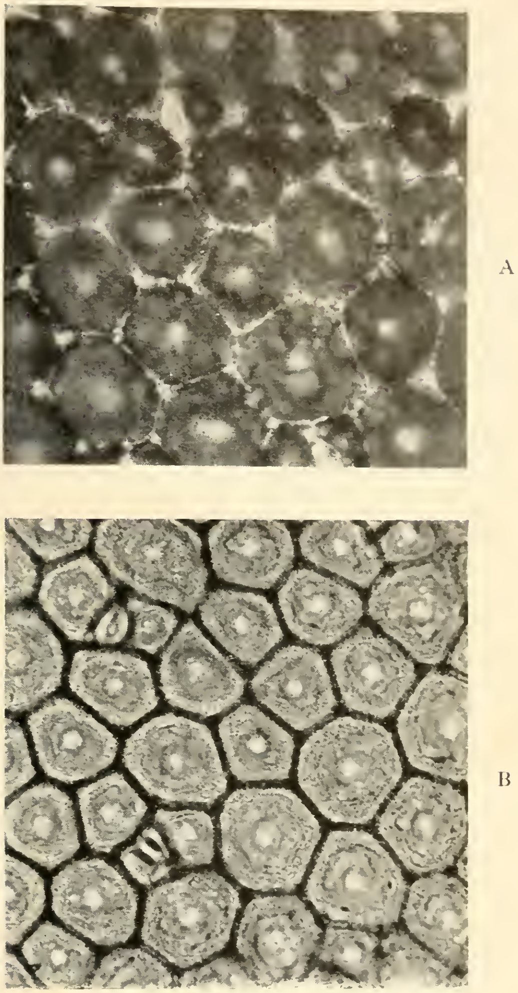

Fig. 999.—*Lithops sp.* Epidermal cells showing focal spots of light on the inner walls. A, In the natural state. B, After decalcification.

the inner tissues and the environment, and they seem to be fundamental to land life, since we find them, or structures analogous to them, in all land plants, from the Bryophyta upwards. From this standpoint their functioning is dealt with in Volume III, in relation both to photosynthesis on the one hand and to transpiration on the other. Here we shall consider them anatomically.

Stomata in land plants are chiefly distributed on the lower leaf surface, a fact which has been interpreted as giving protection against the blocking of the stomatal opening by dust, rain, and dew. There are, however, many exceptions in which stomata occur on both surfaces, especially among those plants, principally Monocotyledons, which have leaves held vertically. Centric and bifacial leaves which do not possess the usual dorsiventral anatomy have stomata distributed more or less over the whole surface, but usually with more on the lower side. Stomata confined to the upper surface only are very rare, except in Grasses like *Ammophila*, with grooved leaves, and in the floating leaves of water plants, where the advantage is obvious. It is not, however, as might be supposed, the direct result of the conditions, since certain water plants, notably *Polygonum amphibium*, grown in air under moist, warm conditions, will produce, in succession, leaves of the submerged type, then leaves of the floating type with numerous stomata only on the upper surface, and lastly leaves of the aerial type with stomata on both sides, but more numerous on the lower side. Here the difference is clearly not due to the direct action of the environmental conditions, but is the result of changes in the inner organization of the plant, the causation of which is unknown, but which fit in satisfactorily with the normal characteristics of the plant's habitat in water of medium depth. This is an important aspect of the question of adaptation to which we shall refer in Volume IV.

The numbers of stomata per unit area of leaf surface are very variable but are normally between 50 and 400 per sq. mm. Salisbury, comparing British plants of various habitats, found that the frequency tended to be greater in plants from dry, exposed situations than from humid places, though the individual stomata were usually smaller in the former case. This difference he showed to be correlated with differences in the growth of the leaf as a whole. During the primary phase of development in the leaf primordium the number of stomata is determined and their initial cells are formed, but the subsequent phase of expansion determines their spacing and hence their frequency.

When leaves from plants of the same species, growing under different conditions of humidity, are compared, it is found that the ratio of the number of stomata to the number of epidermal cells per unit area is remarkably constant. Salisbury expressed this by the formula :—

$$I = \frac{S}{E + S} \times 100$$

and called I the **stomatal index**. Here, S stands for the number of stomata and E for the number of epidermal cells per unit area, the latter being chosen to avoid the apex, the margins and the large veins. It implies that the proportion of superficial cells which become stomata is constant for the species, and the index is, indeed, independent of habitat and of the age and position of the leaf, and is so specifically constant that it may be used as a diagnostic character in the separation of closely related species.

These important observations of the relation of frequency to the amount of expansion during leaf development, serve as a clue to the variations of frequency not only between different plants, but between different parts of the same plant. The frequency, especially in herbaceous plants, increases with the height of a leaf above the ground, and in trees with its distance from the base of the branch, that is inversely to its age. Likewise, there is often an increase of frequency from the base to the tip of the lamina and from the midrib towards the margins in the individual leaf.

Stomata in Dicotyledons are characteristically orientated at random (Fig. 1000), that is to say, their long axes do not lie in any particular direction. Careful analysis has shown, however, that this irregularity is only apparent and is not related to the irregularity of the epidermal cells (Fig. 1001), but

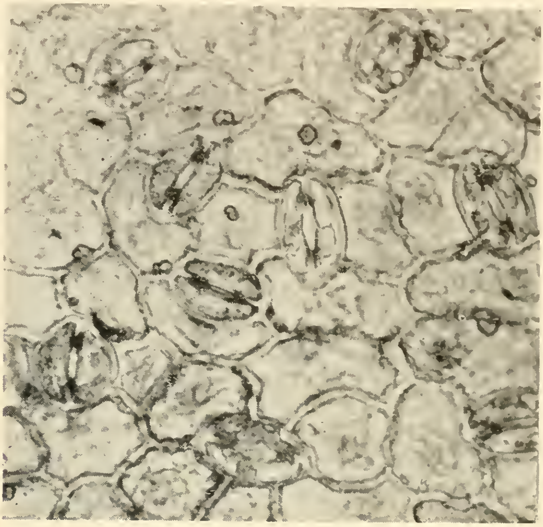

FIG. 1000.—*Forsythia suspensa.* Epidermis from the lower surface of leaf showing random orientation of stomata.

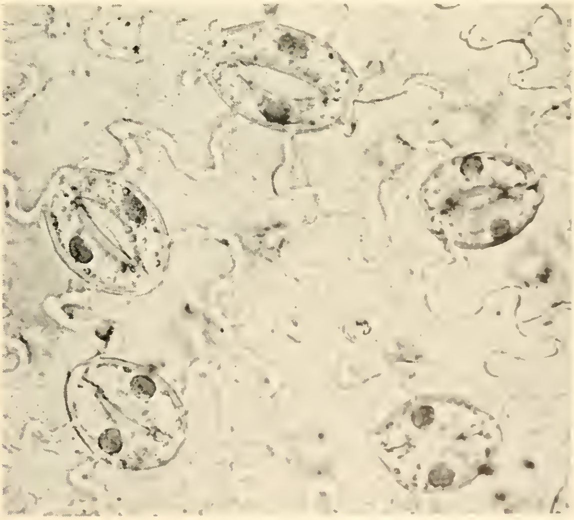

FIG. 1001.—*Paeonia corallina.* Lower epidermis of leaf showing random distribution of stomata and the irregularity of the cell walls.

is, in fact, closely correlated with the direction of the underlying veins in the mesophyll. Here again differential growth rates are probably responsible. More rapid stretching of the leaf tissue along the veins is shown by the more elongated epidermal cells usually formed above them and this may account for the elongation of stomata in the same general direction.

The linear leaves of many Monocotyledons, in which growth is continuous from the leaf base, usually have the epidermal cells and the stomata in longitudinal rows (Fig. 1002), the latter also having their long axes regularly in the same direction. Monocotyledons, such as *Arum*, with net venation, have randomized stomata like those of Dicotyledons. Transversely orientated stomata are uncommon and are nearly always associated with reduced leaves and xeromorphic structure.

FIG. 1002.—*Iris pallida.* Epidermis of leaf showing narrow elongated cells and stomata arranged longitudinally.

The differentiation of stomatal mother-cells from epidermal cells begins at a very early stage of leaf development. It involves that rare occurence, the division of a cell into two markedly unequal portions, a large cell which becomes epidermal and a smaller cell, always on the side towards the apex, which becomes a stomatal initial cell.

The first differentiation of stomata is usually coincident with the beginning of expansion in the leaf rudiment. It is not simultaneous all over the surface, but begins near the leaf apex, the differentiation in other parts being concurrent with the appearance of air spaces in the mesophyll. Stomata are formed successively for some time, the earliest to appear showing an orientation related to the direction of growth tensions, while those which appear later are seemingly irregular in alignment.

The stomatal initial cell is in most cases also the mother cell of the stoma, but in certain families the initial cell may divide once or several times, producing a stomatal mother cell surrounded by a variable number of **subsidiary cells.** The majority of families, however, produce subsidiary cells, if at all, by sub-division of the neighbouring epidermal cells and the initial cell divides only once to form the two **guard cells** of the stoma. Between these the pore appears, owing to the splitting of the wall which separates them. There is much variation in the details of stoma formation, many of which are peculiar to certain families and can be used as systematic characters.

When first formed the guard cells equal the epidermal cells in depth, and lie in the same general plane. The sunken position of many stomata is due to later growth of the epidermis and sometimes to its periclinal division into two or more layers.

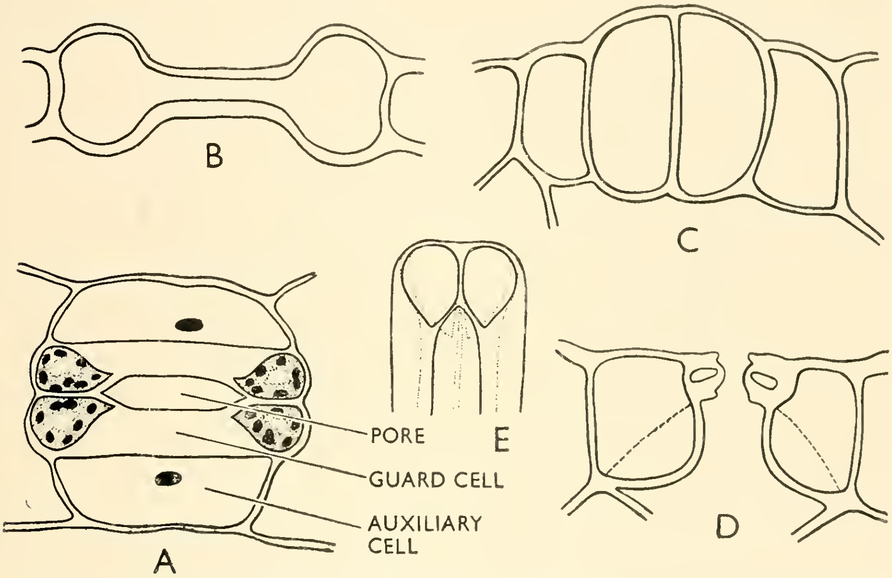

FIG. 1003.—*Zea mais.* Structure of the stoma. A, Surface view. B, Longitudinal section of guard cell. C, Transverse section through the ends of the guard cells. D, Transverse section through the stomatal pore and middle of the guard cells. E, Surface view, guard cells in open and closed positions. (*After Copeland.*)

The shape of the guard cells is remarkably uniform, though they vary considerably in size. They are curved in two directions. Firstly, there is the obvious concavo-convex curvature which separates them from each other, except at their ends. This curvature is variable and affords the means of controlling the stomatal opening. Secondly, there is a curvature less easily seen, perpendicular to the surface, the extremities of the cells being turned somewhat downwards. This curvature does not vary as the first does. The upper and lower walls are highly thickened, while the lateral walls are relatively thin.

The Gramineae are remarkable for guard cells of a peculiar pattern (Fig. 1003). They are straight, not curved, and shaped like a pair of dumb-bells, side by side. The middle portions are highly thickened, while the expanded ends are thin walled. It is the expansion and contraction of these thin walled portions which varies the distance between the cells and hence the width of the stomatal openings.

The mechanism of stomatal movement is not yet fully understood. The turgor pressure in the guard cells varies and with increasing turgor they become more curved and the opening between them widens, while the reverse occurs with decreasing turgor (Fig. 1004). These changes are associated with corresponding changes in their osmotic potential.

The guard cells are unique among the superficial cells in containing green plastids. They are present even in plants grown in the dark, and are also present on the colourless portions of variegated leaves. Starch accumulates in these plastids, even in plants which do not form it in the mesophyll cells, and this starch is subject to reversible hydrolysis into sugars, presumably by enzyme action, without, however, any change in the total carbohydrate content of the cells. The carbohydrate is apparently not manufactured by the guard cells, but seems to be obtained from the mesophyll and it is even doubtful whether their plastids are photosynthetically functional. The starch content is greatest in the early morning hours and decreases in daylight, with a concomitant rise in the osmotic potential of the cell sap and increased opening of the stomata. The reverse changes occur during the evening and no further change appears to occur during the night. It is supposed that light affects the balance by causing absorption of carbon dioxide by the plastids thus increasing the alkalinity of the cell sap, and thereby activating the amylase enzyme to hydrolyse the starch. With decreasing light, the carbon dioxide produced by respiration begins to accumulate, the cell sap becomes more acid and the resynthesis of starch is favoured, resulting in a drop of osmotic potential and hence of turgor.

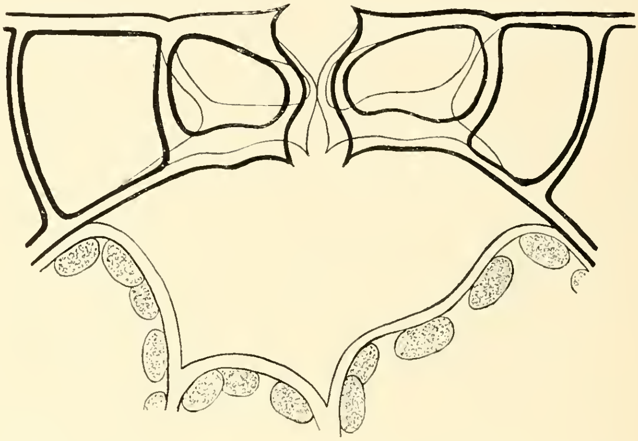

FIG. 1004.—*Vinca rosea*. Diagram of a section through a stoma. Thick lines show the position of the guard cells when the stoma is open. Thin lines indicate the changes in the position of the cell walls which bring about the closing of the stomatal pore. (*After Kohl.*)

This account of the reactions, though it is consistent with observations and with experimental results, so far as they go, must be regarded as still hypothetical, since it has not been definitely proved that photosynthesis occurs in stomatal plastids, nor has the presence of amylase in the guard cells been demonstrated.

Scarth considers that the opening and closing movements are too rapid to be accounted for by enzymatic reactions, and considers that the changes of acidity, which do take place, affect the imbibitional swelling of the cell colloids and that the changes of turgidity are, at least in part, due to changes of water content due to colloidal imbibition. As the water drawn in to the guard cells must come from the leaf tissues, it follows that the possibility of movement will be affected by the water content of the leaf as a whole. A decrease of mesophyll water content, due to wilting, will increase the osmotic potential of the mesophyll cells and when this has passed a certain value it will no longer be possible for the guard cells to withdraw water from them and the stomata will remain permanently shut, thus minimizing the further loss of water from the leaf.

Finally it may be said that recent observations have detected a rhythmical pulsation in guard cells, with a fifteen-minute period, which is even maintained for twelve hours in continuous light. To what this is due is not known, though a short-period opening and closing can be produced, experimentally, by variations of tissue water content, under extreme environmental conditions.

The classic researches of Loftfield have shown that stomata do not all react similarly to light and that they generally conform to one of three types.

Type 1.—Typical of Grasses, including the cereals. During the day the stomata may open and close rapidly, but they are only open for an hour or two altogether and only under the most favourable conditions. There is no opening at night.

Type 2.—Includes most thin leaved mesophytes.[1] Usually the stomata open all day and close all night. Under less favourable conditions they may close at midday, and under very unfavourable conditions, especially heat and drought, this may extend to the whole day (Fig. 1005). Night opening is the obverse of day opening, so that under very dry conditions stomata may be closed all day and open all night, depending on the water content of the tissues.

Type 3.—The "Potato Type" (Fig. 1006). Under favourable conditions the stomata are open more or less all day and all night, closure being caused by increased evaporation rather than by darkness. With diminished water content they become more responsive to light and then they tend to conform to Type 2.

The stomata of many water plants have no power of movement and remain open even when the leaves are wilted. Immobile and enlarged stomata may also function as **water stomata** through which water is excreted under very moist conditions. They occur principally at the margins of leaves, as in *Fuchsia*, *Tropaeolum* and *Primula*, or at the leaf tips, as in the primary leaves of many Grasses. These water stomata form one of the types of water-secreting structures, or hydathodes (see p. 472).

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[1] Plants living under normal environmental conditions.

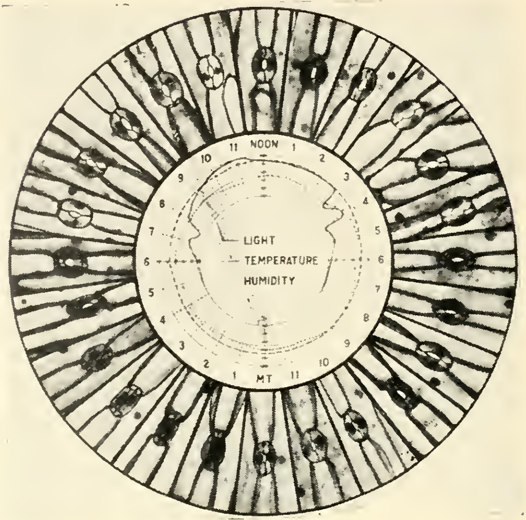


Fig. 1005.—*Allium cepa.* Photographs of stomata showing the cycle of opening and closing during twenty-four hours; correlated with the variations of light, temperature and humidity. Stomata closed, or practically closed, all night and open all day.

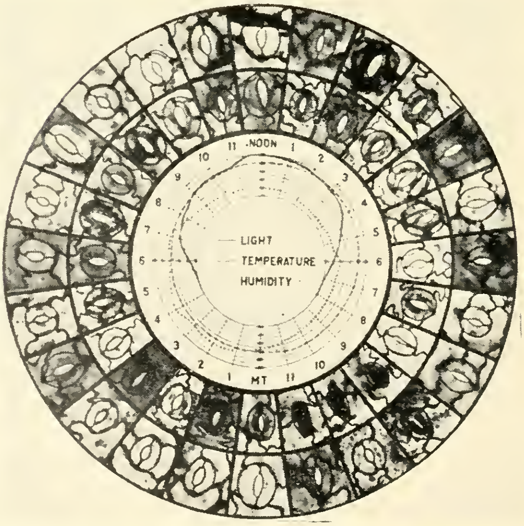


Fig. 1006.—*Solanum tuberosum.* Photographs of stomata, on upper and lower surfaces of the leaf respectively, showing the cycle of opening and closing during twenty-four hours; correlated with the variations of light, temperature and humidity.

(*From Loftfield, Carnegie Institute Publication* 314, *by permission of the Carnegie Institute of Washington.*)

THE MESOPHYLL.

Typically the leaf mesophyll consists of one or more layers of prismatic cells arranged anticlinally, with narrow spaces between them, constituting the **palisade layer**, while below this lies the **lacunar** or **spongy tissue**, made up of irregularly shaped cells, between which is a connected system of large intercellular spaces, which almost completely surround the cells and contain an internal atmosphere which is kept in communication with the exterior air through the stomata.

The elongation of the palisade cells has been compared with the elongation of epidermal cells into hairs, and it has been suggested that both may be due to the operation of similar factors, such as strong light or rapid transpiration associated with exposure, which check the growth of the leaf in area and promote the lateral extension of the cells. There may be some truth in this, but it is obviously not a complete explanation and further information is needed.

The fundamental structure of the mesophyll is found in all normal dorsiventral leaves, both dicotyledonous and monocotyledonous, though in the latter the palisade layer is usually less developed than in the former. Leaves of the grass type, however, are exceptional. They have parallel veins which lie close together, with ribs of sclerenchyma above and below each vascular bundle. This cuts up the mesophyll into a number of independent strips, in each of which there are, at the top and the bottom respectively, two belts of tissue containing chlorophyll, while the central portion is sometimes lacunar in structure, but more often composed of thin-walled, colourless cells which store water.

Dicotyledons may also have a palisade on both sides of the mesophyll. This is formed, for example, in plants with a normally vertical leaf position and in others which grow under such conditions (*e.g.*, on sand) that the under sides of the leaves receive strong lighting (Figs. 1007 and 1008). Such leaves are called **equifacial**, or sometimes **isobilateral**. A further modification of leaf structure is that called **centric**. The extreme type of centric leaf is cylindrical, with all the mesophyll tissue arranged radially round one or more centrally placed veins (Figs. 1009 and 1010). A less extreme type is found in some species, especially of Grasses and Sedges, in which the leaf as a whole is bilateral, but the veins are surrounded by radiating palisade cells, examples being *Papyrus* and *Portulaca*. The truly centric leaf is really a special case of equifacial development, but there is another closely similar type of centric leaf which is derived in quite a different way, by the suppression of the upper surface during development, and the overgrowth of the lower surface, which thus surrounds the whole leaf. They are really extreme cases of the rolled or folded leaf. Such leaves are called **unifacial** (see Fig. 1011). They may be cylindrical, as in *Juncus* and *Scirpus*, or they may be flattened in the vertical plane, as in *Rochea falcata*, but they are always recognizable by the fact that in cross section they show a line of vascular bundles, usually curved into a horse-shoe form or into an almost complete ring, instead of the centrally placed bundles of the truly centric leaf.

The lacunar structure of the mesophyll, though most marked in the spongy tissue, extends to the palisade also, between all the cells of which run clefts connecting with the spaces in the spongy layer. The cells are normally rounded in cross section, and a view perpendicular to the leaf epidermis shows clearly the extent of the intercellular space system in the palisade, which is not so apparent when viewed in the usual transverse leaf section. The size and closeness of the palisade cells varies with external conditions. In leaves growing in sunshine they are long, large, and close together, and in leaves in heavy shade they tend to become short, thin, and loosely arranged. The same is true of the spongy tissue, and the total volume of intercellular space may be twice as great in a shade leaf as in a sun leaf of the same species. The average volume of the internal space is about 20 per cent. of the leaf volume. The internal area of cell surface exposed in the mesophyll is difficult to estimate with any accuracy, but investigations by Turrill established that

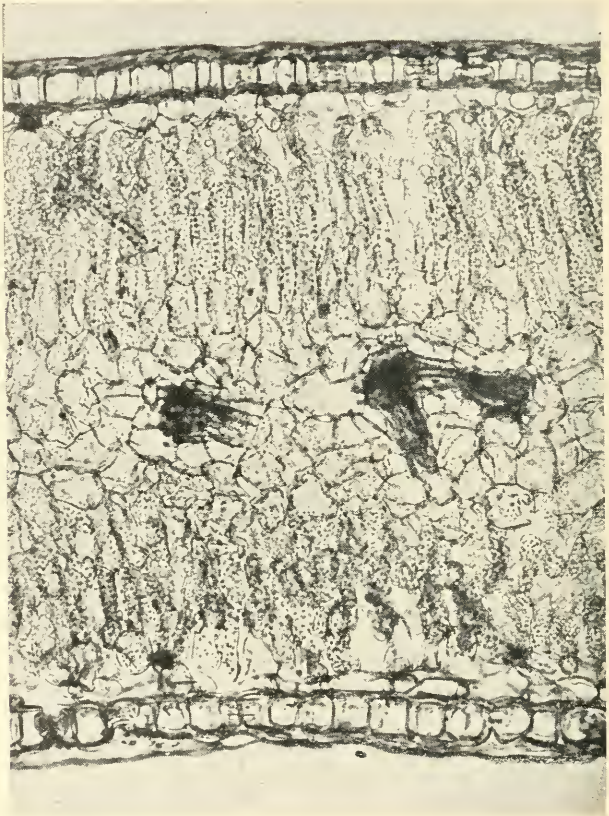


FIG. 1007.—*Eryngium maritimum.* Transverse section of leaf showing equifacial structure.

the ratio (R) between internal and external surface was lowest in shade leaves, with reduced numbers of mesophyll cells, (R = 6·8 – 9·9) and highest in sun leaves of xerophytic type (R = 17·2 – 39·3) the average ratios in mesophytic leaves being between 11·6 and 19·2. Contrary to expectation he found that

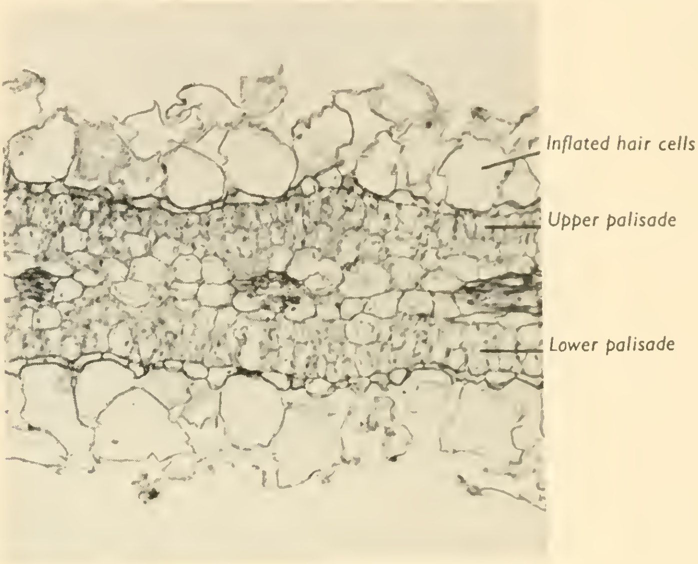


FIG. 1008.—*Obione portulacoides.* Transverse section of leaf showing equifacial structure and protective covering of vesicular hairs on both surfaces.

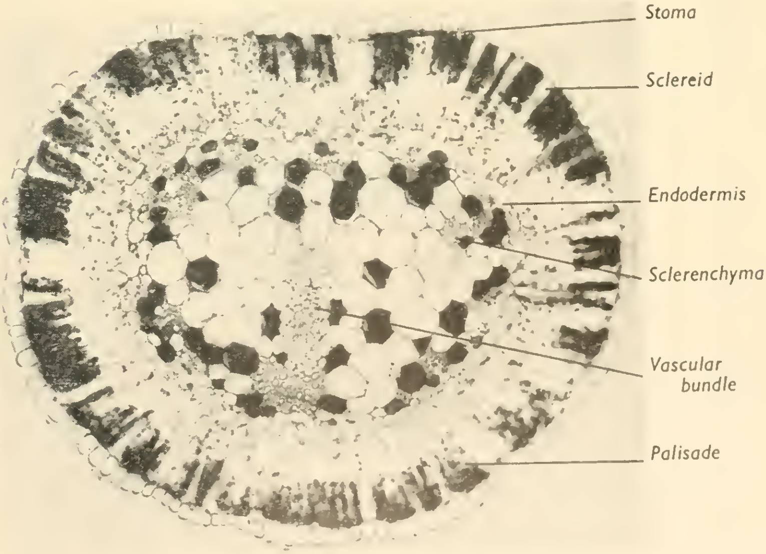


FIG. 1009.—*Hakea pectinata.* Transverse section of leaf showing centric structure.

the palisade tissue exposes from 1·6 – 3·5 times as much free cell surface as the spongy tissue. This is due to the form of the cells which lends itself to close ranking. In spite of variations in the size of the palisade cells, the palisade ratio, which is the ratio of the number of palisade cells to epidermal cells in a unit area, is remarkably constant and is used as a diagnostic character in pharmacognosy (Fig. 1012). This constancy is due to the mode of growth in the young leaf. Cell division ceases first in the epidermis, but the epidermal cells continue to expand, as marginal growth of the leaf continues, after the mesophyll cells have ceased to grow. The latter are, therefore, drawn apart and the intercellular spaces are thus created. Obviously, therefore, wider spacing of the palisade cells will be correlated with larger epidermal cells, and the constancy of the palisade ratio is analogous to the constancy of the stomatal index.

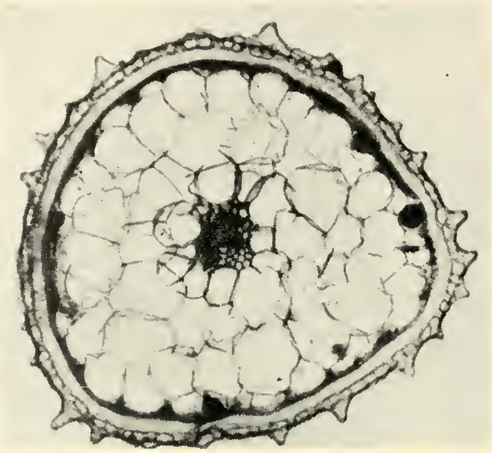
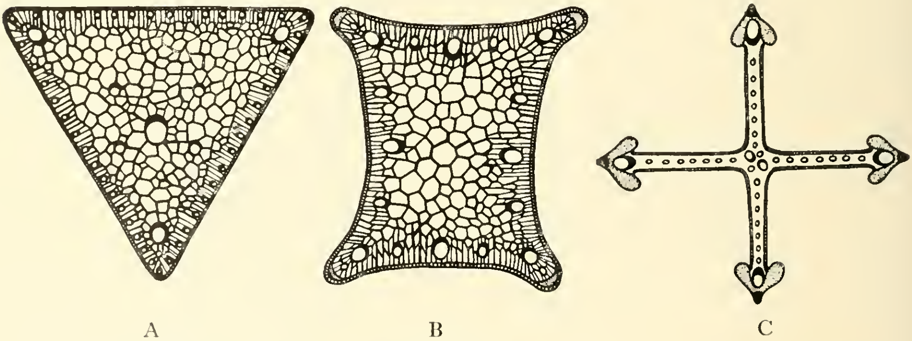


FIG. 1010.—*Salsola kali.* Transverse section of leaf showing centric structure.



A B C

FIG. 1011.—Diagrams showing the structure of unifacial leaves. A, *Butomus umbellatus.* B, *Iris wartani.* C, *Acidanthera platypetala.* (*After Velenovsky.*)

Not only does the palisade layer possess the larger cell surface, but it also contains a much greater number of chloroplasts than the spongy tissue. It also occupies the better lighted side of the leaf, and for these reasons it must be regarded as the principal photosynthetic tissue.

At first sight the cylindrical form of the cells might not seem to be the best fitted for the exposure of the maximal area of chlorophyll to the sun's rays, towards which they present their narrow ends. Vertical light, passing through the epidermal cells is, however, refracted as we have seen above, and passes obliquely into the cells below, thus ensuring the illumination of the longitudinal walls of the palisade cells, and of the chloroplasts which line them. The efficiency of illumination is thus high, and it is increased by internal reflection from the cell walls, which carries the light still further down in deep palisades. There is a general correlation between the depth of the palisade layer and the intensity of the incident light. Leaves growing under intense sunlight may have three or even more superimposed palisade layers. Leaves in the shade have only one layer, and that of slight depth. Indeed in deep shade the palisade may consist of funnel-shaped cells with curved walls and with the apex downwards, the chloroplasts being concentrated at the apex where the light is also concentrated by internal reflection from the cell walls, thus applying the principle of the searchlight in reverse.

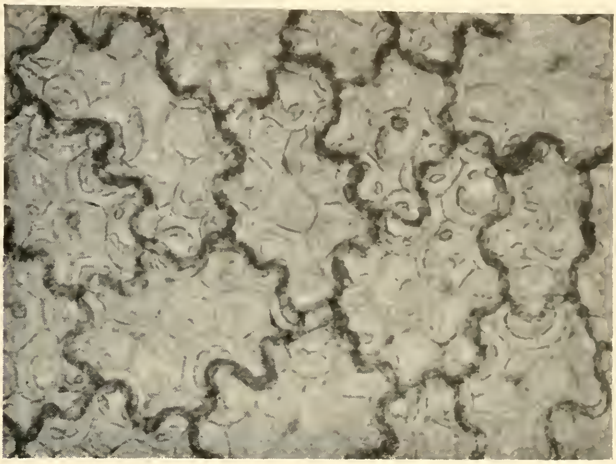


FIG. 1012.—*Helleborus niger.* Epidermal view of the upper surface of leaf showing the relationship of the ends of the palisade cells to the epidermal cells.

We have described in *Pinus* (see p. 672) the flanged mesophyll cells which are characteristic of that genus, and have suggested that they are due to the constriction of the cells during growth by cuticularized rings on the walls. Similar flanged or lobed palisade cells are not uncommon in Angiosperms. The H-shaped type is perhaps the commonest, and occurs widely among the Ranunculaceae. Whether it originates in the same way as in

Pinus is uncertain, but physiologically the effect of the flanges in increasing the internal surface of the cell is identical, and hence the surface available for the exposure of chloroplasts is also increased. Such cells are not confined to the family mentioned above and they occur sporadically in many families, both of Dicotyledons and Monocotyledons (Fig. 1013).

The lacunar tissue plays a subsidiary part in photosynthesis, and it is uncertain whether its cell walls are sufficiently permeable to allow for much gaseous interchange or for the evaporation of water. Lewis has recently shown that the walls of the spongy tissue cells are highly hydrophobic and unwettable by water. They show no tendency to absorb water which is injected into the leaf, though it is taken up by the cells of the veins. These observations have not been extended to the palisade cells, and it may prove that there is a differentiation in this respect between the two layers and that the palisade is the chief seat of transpiration as well as of photosynthesis.

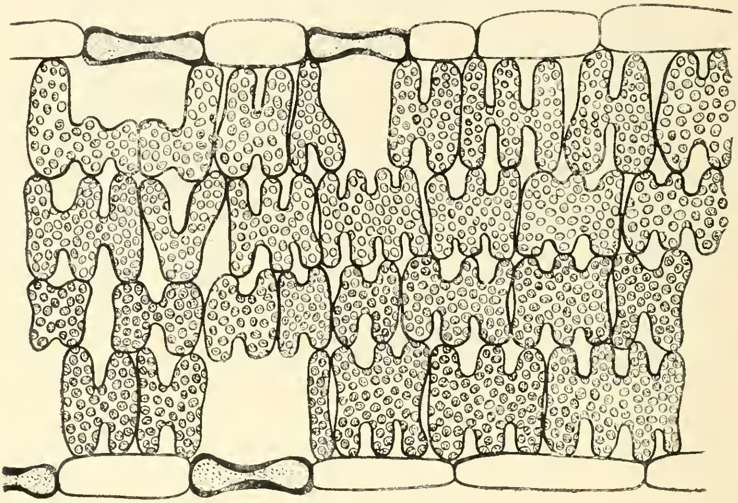


FIG. 1013.—*Triticum vulgare.* Longitudinal section of leaf showing lobed mesophyll cells. (*After Bruner and Weaver.*)

The external cuticle of the leaf is often continued inwards through the stomatal pore and extends as a relatively delicate film over some part of the spongy mesophyll. In some cases there is evidence that it may extend over the whole surface of that tissue, which may account for its unwettable character.

Injury to the mesophyll may induce the growth of tyloses (Fig. 1014) from the spongy cells into the intercellular spaces, blocking them in the same way that the cavities of old vessels become blocked. Mesophyll cells exposed by injury may also form a phellogen and the wounded surface is thereby covered and protected by the development of **wound cork** (Fig. 1015).

The lacunar tissue clearly serves at least two functions ; the intercellular spaces provide a reservoir of air and water vapour which may be of great benefit to the palisade cells as a buffer between them and external conditions, while its cells serve as channels of transport for materials between the palisade cells and the veins. Anatomically this is illustrated by the system of what are called **collecting cells**, that is, mushroom-shaped cells, the flattened heads of which each make contact with the bases of a group of palisade cells. The relative isolation of palisade cells from each other implies that there can be little, if any, lateral transport between them, and that carbohydrate translocation from the palisade layer must be through the base of each cell individually. The rest of the spongy parenchyma forms an anastomosing system of pipe lines connecting with the veins, which are both the source

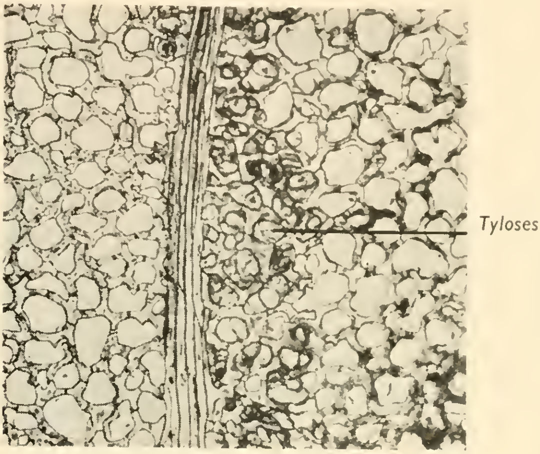


FIG. 1014.—*Berberis nervosa.* Horizontal section through the spongy mesophyll showing tyloses in the intercellular spaces. (*After Wylie.*)

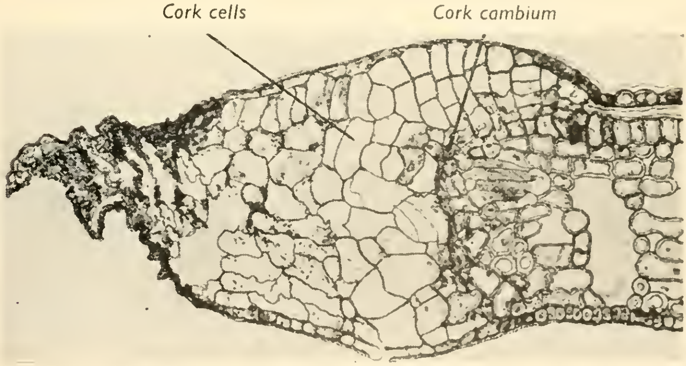


FIG. 1015.—*Berberis nervosa.* Transverse section through the injured margin of a leaf showing the development of wound cork. (*After Wylie.*)

of the water supply and the channels of translocation of organic materials from the leaf to other parts of the plant.

The veins are always differentiated at the boundary between the palisade and the spongy layer, and are hence practically median. Each vein is surrounded by a sheath of elongated parenchyma, normally devoid of chlorophyll, which is one cell thick in the finer veins, but increases in thickness as the leaf base is approached, where the sheath cells pass into the massive parenchymatous coat of the midrib (Fig. 1016), which in turn is continuous with the ground tissue of the petiole. There appears to be a concentration of sugars in these sheath cells, and they are sometimes called the glucose sheath. They are probably important in translocation, especially at the vein extremities, where the amount of vascular tissue in each vein is very small. The question of an homology between these vein sheaths and the endodermis cannot be definitely answered. A typical endodermis, with Casparian bands on the cell walls, does occur in the leaves of several families, notably the Primulaceae, the Plantaginaceae and the Rosaceae. At the leaf base it may even be secondarily suberized, but among the smaller veins it is usually irregular and incomplete, and the characteristic band on the cell walls is absent from the smallest veins. In the majority of families an endodermis is altogether absent from the leaf.

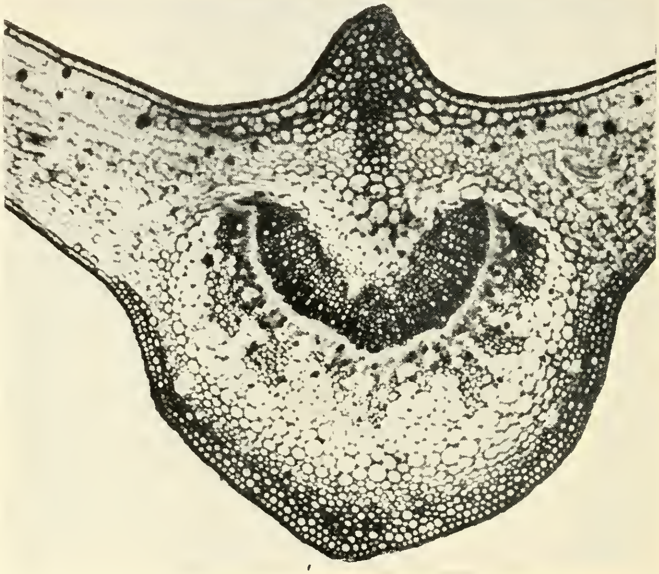


Fig. 1016.—*Laurus nobilis*. Transverse section through the midrib of a leaf showing a U-shaped vascular bundle surrounded by a parenchymatous coat.

The free end of each vein is formed of a single tracheid, which is often enlarged (Fig. 1017). The phloem stops short of the end, and the last phloem cells are peculiar, and may be regarded either as enlarged companion cells or as sieve-tube mother cells which have not divided into distinct sieve-tube and companion cell units. The vein sheath extends like a cap over the end of each vein and is thus continuous.

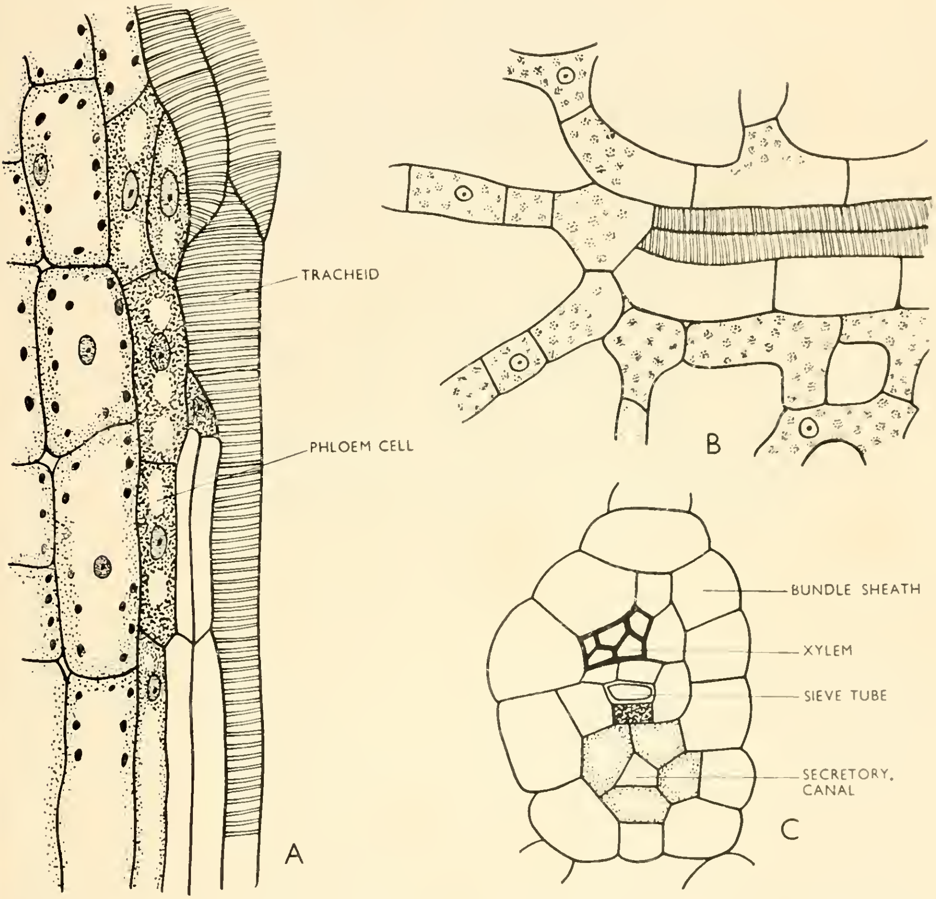


Fig. 1017.—Bundle endings in the mesophyll. A, *Fuchsia globosa.* Bundle ending in a leaf tooth. B, *Ficus elastica.* Bundle ending of two rows of tracheids and one row of phloem parenchyma. C, *Aralia sieboldii.* Transverse section through a bundle end. (*After Haberlandt.*)

The vascular tissues of the veins are characteristically arranged with the xylem uppermost. This is a necessary consequence of the position of these tissues in the stem bundles, for as a leaf trace bundle turns outwards into the petiole, its xylem becomes uppermost and this position is usually maintained, without torsion, through the petiole into the lamina.

Many accessory structures may occur in the mesophyll. Crystal sacs, containing Calcium oxalate crystals are common, while cystoliths in specially enlarged cells are characteristic of the Urticaceae. Glandular sacs and canals occur in certain families and contain either mucilage or aromatic terpenes. Where the sacs are large they form colourless points in the tissue, as may be seen with the naked eye in such species as *Hypericum perforatum*, which gets it specific name from this circumstance (Fig. 1018).

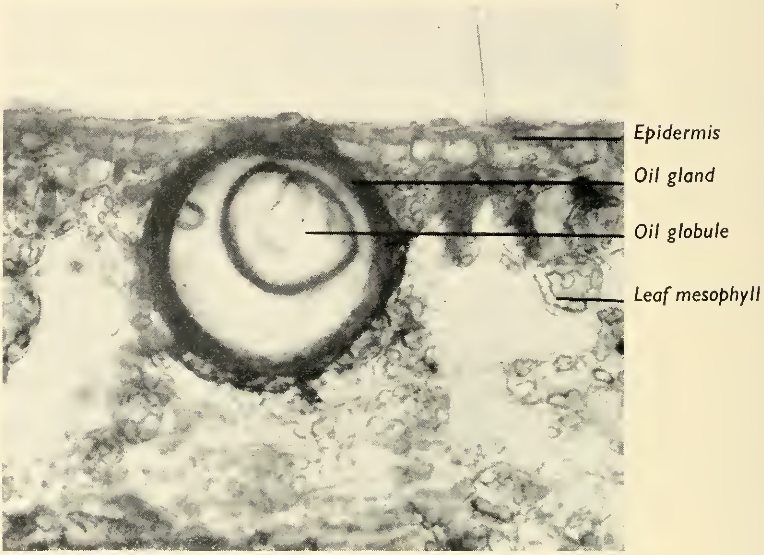


FIG. 1018.—*Myrtus communis*. Transverse section of leaf showing a large oil gland in the mesophyll.

Sclereid cells, often of complex shape also occur, particularly in those hard-leaved plants such as *Camellia* and *Olea*, which are called **sclerophyllous**. The orientation of these sclereids is usually definite in each case, lying either transversely, like pillars across the mesophyll, or longitudinally, in the spongy mesophyll or between the upper epidermis and the palisade layer (Fig. 449).

THE PETIOLE.

In transverse section petioles are seldom perfectly circular, but are flattened or grooved on the upper (adaxial) surface. The two rims of the groove frequently expand gradually as the leaf blade is approached and pass insensibly into the base of the lamina. Not infrequently the rims have the laminar structure all the way down the petiole, which is thus fringed with assimilating tissue, which may even continue some distance down the stem and is then called **decurrent** (Fig. 1019). Where the leaf margin is toothed, the teeth may also be continued along the petiolar fringes and in some plants, such as *Viburnum* and *Cerasus*, the teeth on the petiole are transformed into one or more **extra-floral nectaries** ; small, stalked, cup-shaped glands which produce nectar (See Fig. 1020). Other nectaries are produced on the leaves of many species, usually on the under side of the blade or of the stipules, by local modifications of the epidermis. The secretory surface layer in all cases is called the **epithem**. The biological significance of such nectaries is doubtful. The amount of nectar and its sugar content vary considerably. Sometimes

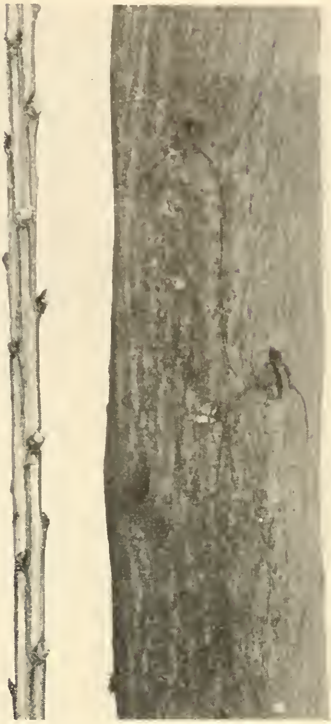


FIG. 1019.—*Sarothamnus scoparius.* Young and old stems showing the persistent decurrent leaf bases.

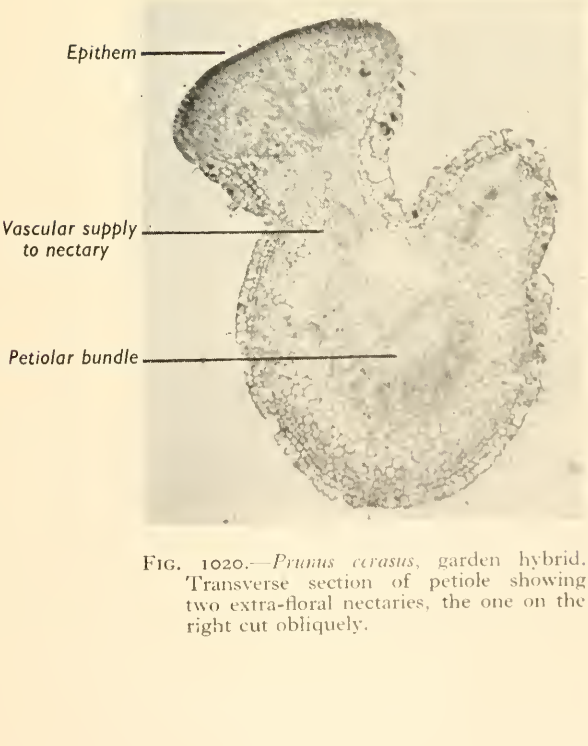


FIG. 1020.—*Prunus cerasus*, garden hybrid. Transverse section of petiole showing two extra-floral nectaries, the one on the right cut obliquely.

they are frequented by honey bees but in other cases only by flies and ants, which may in this way be diverted from the flowers, where their visits might be harmful.

The ground tissue of the petiole is parenchymatous, often with a superficial zone of collenchyma, or, in Monocotyledons, of sclerenchyma. The **pulvinus**, when present, is simply a swollen leaf base and differs only in the relatively greater amount of parenchyma present. Its vascular anatomy is similar to the rest of the petiole. Pulvini which execute movements, such as those of *Mimosa pudica* (see Volume III), usually show some difference in the parenchyma on their upper and lower sides, that on the side which becomes concave on stimulation being thinner walled than that on the other side. There are also numerous pits present and protoplasmic connections between the cells. Strictly speaking the term pulvinus, though generally applied to the swollen leaf base, includes nodal swellings on the stem, especially where these are the seat of movement, as in Polygonaceae and Gramineae.

The vascular strands of the petiole are not as a rule segregated into a distinctive stele, though an endodermis may be present and is sometimes, as in *Primula*, *Valeriana*, and *Plantago*, continued into the lamina, as we have mentioned before.

It must be remembered that the whole leaf rudiment is essentially a dorsiventral structure and this symmetry persists, not only in the lamina but also in the petiole, which is morphologically a lower portion of the midrib on which the ventral (*i.e.*, adaxial) layer of the rudimentary tissue, that which higher up forms the lamina, has been arrested at an early stage. The petiole therefore, like the midrib, belongs to the dorsal side of the leaf, and its vasculation is dorsiventral, and represents a modified leaf type, not a stem type.

When the lamina has pinnate venation, with a single main vein, the number of bundles in the petiole is small, normally one to three (Fig. 1021). Where there is only one it may be expanded laterally into a broad band (Fig. 1022). In palmately veined leaves the number may be greater, but in all normal cases the course of the bundles is parallel and they form an arc, open on the upper side. This is the fundamental petiolar type, corresponding to the arc structure of the petiolar traces in the Pteridophyta. A circular radial arrangement of the trace bundles is found in the middle portion of the petiole in certain plants, notably in *Fatsia* (Fig. 1023), but it is a secondary derivative arrangement, produced by the branching and displacement of bundles in the arc, and the normal arc arrangement is seen at the base and top of such petioles, where the dorsiventral character is manifest.

It has been claimed, on the basis of comparative studies, that the three-bundle type of petiole is primitive among Angiosperms and that the single-bundle type, associated with pinnate venation, is derived from it. The suggestion is that originally the three traces passed directly and separately into the broad base of the lamina (Fig. 1024), but that the greater flexibility attainable with a petiole led to the lateral contraction of the base of the lamina and the association of the three traces close together, leading to the eventual

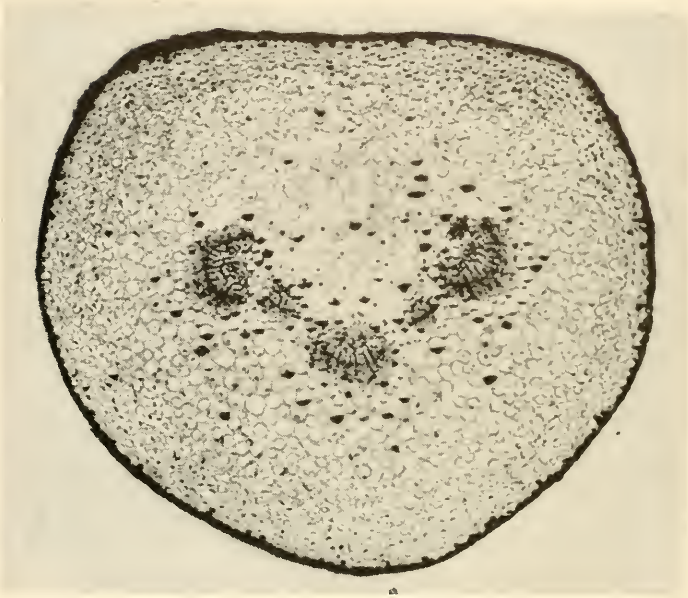


FIG. 1021.—*Aucuba japonica.* Transverse section of petiole showing three main vascular bundles.

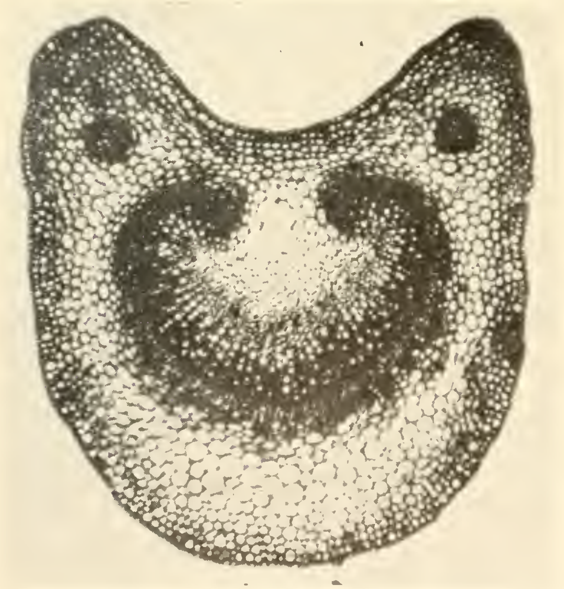


FIG. 1022.—*Syringa vulgaris.* Transverse section of petiole showing a single main vascular bundle in the form of an incurved band. Two subsidiary bundles occur in the upper corners.

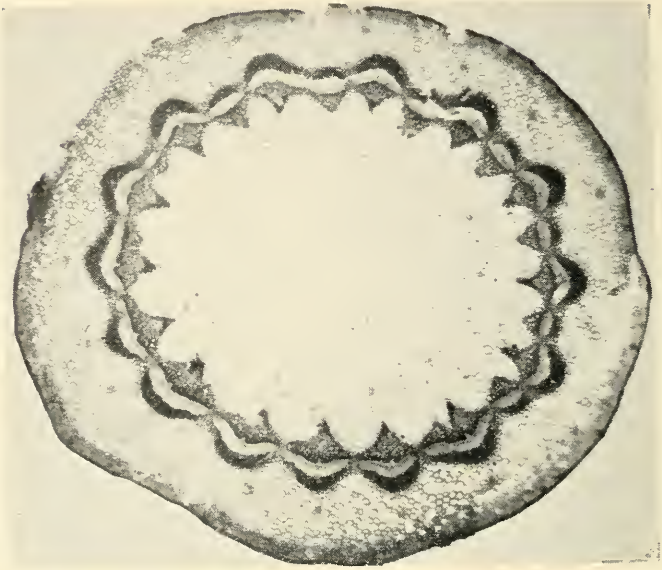


FIG. 1023.—*Fatsia japonica.* Transverse section of petiole showing a complete ring of vascular bundles.

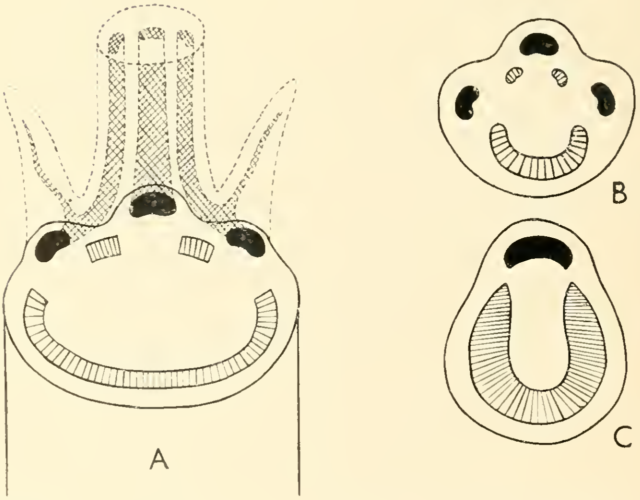


FIG. 1024.—Diagram of leaf traces. A, Three-dimensional diagram of the hypothetical primitive three-trace supply to the leaf, with stipular offshoots. B, Transverse section of the node of a trilacunar trace. C, Transverse section of the node of a unilacunar trace. (*After Sinnott and Bailey.*)

disappearance of the lateral traces either by abortion or by fusion with the median trace. Certainly the three-trace type is very widespread, not only in palmate but also in some pinnate leaves.

Salisbury has shown that in general terms there is a positive relationship between the amount of xylem developed in a petiole and the size of the leaf blade. The proportion of petiolar xylem is greater in mesophytic leaves and less in those which show xeromorphic protections, such as hairy coats. It is, therefore, presumably due to differences in the transpiration rates from different leaves. Such a relationship has an obvious physiological importance and it is significant that the leaf controls its own supply channels. Thoday has shown that the control extends beyond the petiole, and includes a region of influence, which is delimited both longitudinally and tangentially, in the vascular zone of the stem.

In the region just below the node the leaf trace passes inwards obliquely through the cortex and enters the vascular zone, where it may either maintain its independence for several internodes downwards or may unite quickly with the other components of the zone. In the independent part of its course its growth is correlated with the growth of its leaf, as it is in the petiole, and ceases when the leaf is full grown. There is little radial cambial growth and what there is is largely parenchymatous, which may be necessary mechanically, to allow for the outward bending of the trace towards its leaf. The mechanical correlation is probably not perfect, and the withering of lower leaves is usually due to the straining or even the breakage of their trace bundles by secondary growth of the stem wood. The traces of deciduous leaves are, of course, only active in the stem of the current year. In the older stem the trace bundles remain embedded in the woody zone, in which they are completely merged, continuing to grow in harmony with the general growth of the stem, *i.e.*, under apical control. The traces of evergreen leaves remain active for several years, during which secondary stem wood is formed outside their point of origin, but with this wood they have no connections, nor are they continued outwards after the death of their leaves, as happens in some Conifers, notably in *Araucaria*, where traces of old leaves may persist across the secondary wood for many years.

LEAF FALL.

The dropping both of deciduous and evergreen leaves at the end of their life period is an active process known as **phylloptosis**, and is due to the formation of a definite separation zone or **abscission layer** at the base of the petiole. Without this preparation severance does not take place, as may be seen by the persistence of dead leaves on a withered branch, after all the leaves of other living branches have been shed.

The primary phenomenon in leaf fall is the production across the base of the petiole of a separation layer of cells with dense contents, either with or without a renewal of active cell division (Fig. 1025). The middle lamellae of cells in this layer swell and dissolve, thus allowing the cells to separate and causing the detachment of the leaf. In the simplest cases this is all that happens up to the time of separation, but subsequently in the simplest cases and in all others also before separation, there is produced a protective layer on the inner side of the separation layer, which remains as a cover to the scar after leaf fall. This layer is characterized by ligno-suberization of its walls, and its formation may sometimes, though not always, involve cambial activity. Later, a phellogen appears on the inner side of the protective layer and a periderm is formed which is continuous with the stem periderm. There is also, in some plants, an additional lignified layer, which is formed on the outer side of the separation layer. This is shed with the petiole.

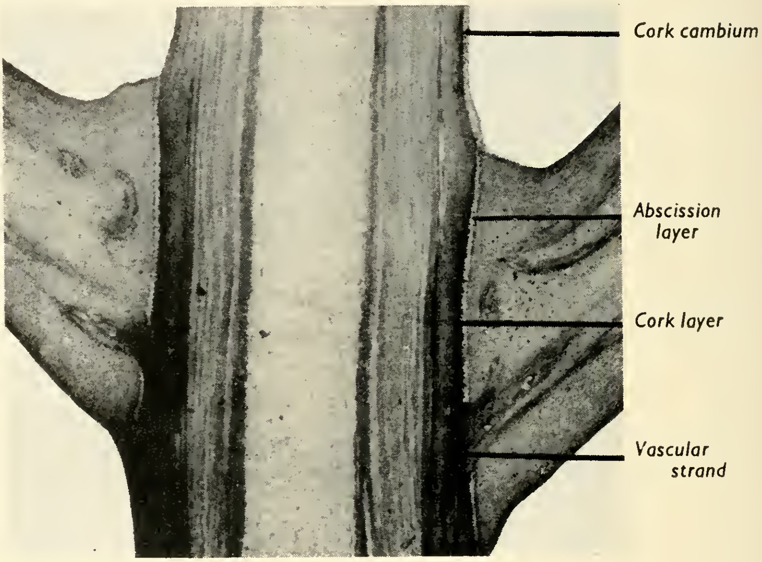


FIG. 1025.—*Aesculus hippocastanum.* Longitudinal median section through a node with two leaf bases, showing the development of the abscission layer prior to leaf fall.

The vascular elements are not interrupted by these layers across the petiole and they are independently sealed off, firstly by the formation of tyloses or of wound gum or of both, and ultimately by crushing, when the growth of the new phellogen begins. The sealed-off ends of the bundles usually remain visible and are characteristic features of the **leaf scar**, which is left on the stem when the leaf has dropped (Fig. 1026).

MODIFICATIONS OF LEAF FORM.

(Modifications associated with special conditions of the environment are dealt with separately in Volume IV).

1. *Leaf Spines.*—Leaves of any type, including stipules, may be spinose, and all stages of modification may occur, from foliage leaves like that of the Holly (*Ilex*) in which the spines are merely hardened teeth at the apex or on

the margins of the lamina, to completely reduced, non-chlorophyllous spines, such as the larger spines of *Opuntia* and other Cacti, which are considered to be extremely modified leaves.

Intermediate conditions are common. Small leaves or phyllodes ending in a sharp point are scarcely to be distinguished from spines (Fig. 1027). The same plant may produce both typical flattened leaves and cylindrical spinose ones, as in many species of *Hakea*, or individual leaves may change from an assimilatory function to spines as they grow older. This happens in some Leguminosae, notably species of *Astragalus*, where the leaflets of the compound pinnate leaf drop off, while the rachis persists and becomes a long spine. The pinnately divided leaves of the climbing Palm, *Calamus*, show a gradual transition from the foliar to the spiny condition as the tip of the very long rachis is approached (Fig. 1028). The spiny segments are directed obliquely backwards and are, in this case, the plant's chief means of attaching itself to its supports in climbing.

FIG. 1026.—*Acer pseudoplatanus.* Portion of a stem showing V-shaped leaf scar and axillary bud transformed into a winter bud.

The genus *Berberis* shows a curious relationship of leaves and spines. At the base of young shoots each node bears a single leaf, usually with a spiny margin, and two small stipules. Higher up the shoot the leaves diminish in size, the marginal spines becoming more prominent, until they are reduced to one or sometimes three spines. The stipules elongate and likewise become

FIG. 1027.—*Carduus crispus.* Plant showing numerous foliar spines.

FIG. 1028.—*Calamus extensus.* Portion of a leaf showing the transition from foliar pinnae to woody spines towards the apex.

spiny. The axillary buds, on the other hand, develop their basal leaves precociously, so that a group of foliage leaves appears to be axillary to a group of spines (Fig. 1029). The groups of three spines at each node on the stem of the Gooseberry, *Ribesura-crispa*, are superficially similar to those of *Berberis*, but they arise below the foliage leaves and are probably outgrowths of the leaf base (Fig. 1030).

The opposite condition is illustrated by *Citrus*, where the leaves of the long shoots are normal, but one or two of the basal leaves of the axillary buds become spines, which appear, therefore, to be axillary to the leaves and were formerly classed as branch thorns (Fig. 1031).

Purely stipular spines are not uncommon. They occur in the succulent species of *Euphorbia* and also in the arboreal Leguminosae, *e.g.*, *Robinia* (Fig. 1032), and especially *Acacia*, in some species of which the spines become very large and hollow, and afford shelter to ants (see Volume IV).

2. *Leaf Tendrils.*—Either the whole leaf, or any part of it, including the stipules, may become modified into a tendril. Sometimes a part may act as a tendril with little or no modification from the normal form, as for example the petioles of *Tropaeolum* and of *Clematis*, or the elongated leaf tips of *Gloriosa*, but often there is some degree of reduction.

It is not unusual to find that the terminal leaflet, or a number of leaflets of a pinnate leaf, become reduced and more or less elongated into tendril form. In *Cobaea scandens* several leaflets are thus altered, their stalks forming the actual tendrils, while the reduced blade of each leaflet forms a small hook at the end of each tendril (Fig. 1033). The Garden Pea affords another familiar example of such a modification of part of a compound leaf (Fig. 1034), while in *Vicia faba* the terminal tendril has itself become vestigial. In these and in most other such cases the blade of the tendril leaflet has disappeared, but in *Mutisia* the laminar development is unaffected and the tendril appears to be a prolongation of the midrib of an otherwise normal leaf, an example of progressive, as contrasted with regressive modification (Fig. 1035).

Less common is the modification of the entire leaf into a tendril. In *Corydalis claviculata* the change from leaves to tendrils takes place by stages, from the base of the shoots upwards, so that a proportion of the leaves remain normally functional, but in *Lathyrus aphaca* all the leaves have become tendrils, and the assimilatory function has been taken over by the enlarged stipules (Fig. 1036).

The morphology of the tendrils in the Cucurbitaceae has been much discussed, but there seems reason to regard them as, in some cases at least, leaf tendrils, which represent modifications of the basal cataphyll or two basal cataphylls of the axillary bud. Another suggested explanation is that they are themselves axillary shoots which end in a leaf tendril. Abnormally they may form a terminal leaf blade, which is not discordant with either view.

One of the most puzzling cases of tendril formation is that found in the genus *Smilax*, in which two tendrils are attached to each leaf, one on each side of the petiole (Fig. 1037). Each tendril contains a ring of bundles essentially like that of the petiole itself, and according to Arber's interpretation they are

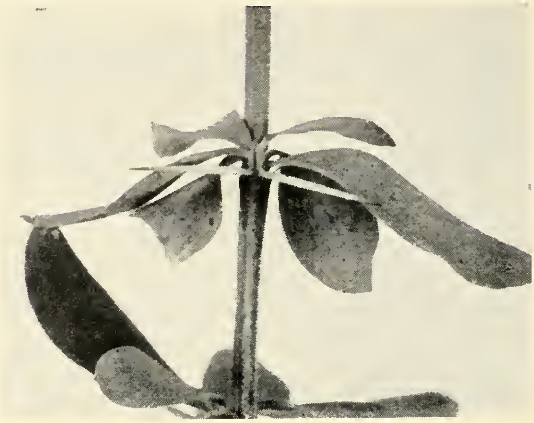


FIG. 1029.—*Berberis aggregata.* Node showing a tripartite spine formed from the leaf and stipules. The leaves of the axillary bud are developed precociously.

FIG. 1030.—*Ribes uva-crispa.* Shoot showing spines developed from the leaf base.

FIG. 1031.—*Citrus trifoliata.* Shoot showing spines developed from the basal leaves of the axillary buds.

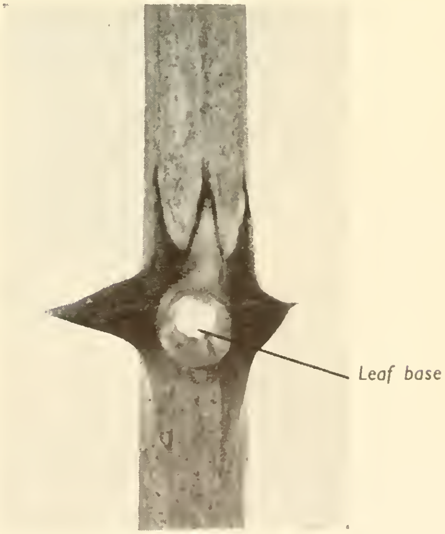


FIG. 1032.—*Robinia pseudacacia.* Node showing stipular spines.

due to chorisis, that is to say, splitting of the petiole rudiment so that there are, in effect, three petioles to each leaf, only the median one of which bears a lamina. A parallel is found in some Dioscoreaceae with compound leaves, in which, however, each of the petiolar members ends in a lamina.

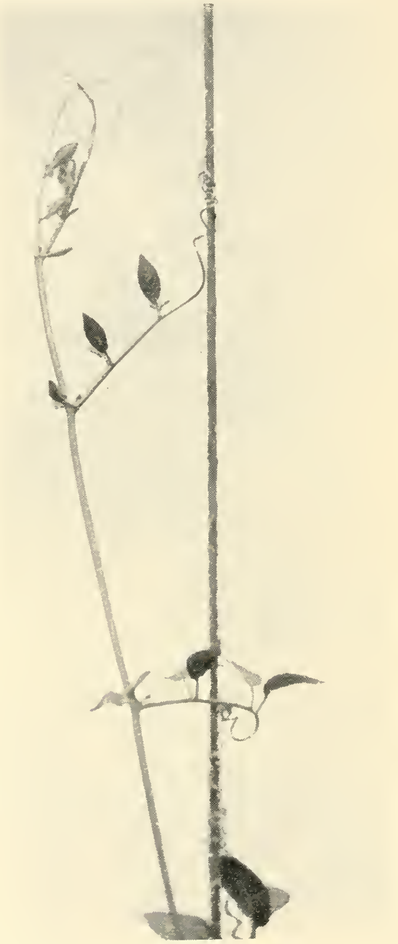


FIG. 1033.—*Cobaea scandens.* Branch showing tendrils formed from distal leaflets of the compound leaf.

3. *Storage Leaves.*—The best known examples of these organs are the scales of bulbs. The latter vary greatly in the number of such scales they contain, from one only, in some species of *Allium*, to the bulbs of *Lilium auratum* with upwards of a hundred scales. The scales likewise vary in their nature. In the bulbs of *Tulipa*, *Saxifraga granulata*, *Fritillaria*, *Gagea* and *Allium cepa*, the common Onion, the scales are cataphylls, that is, modified leaves; but in *Narcissus*, *Galanthus*, *Ornithogalum* and many other genera,

FIG. 1034.—*Pisum sativum.* Shoot showing tendrils formed from distal leaflets of the compound leaf. The stipules are enlarged and function as assimilatory organs.

FIG. 1035.—*Mutisia ilicifolia.* Shoot showing tendrils formed by a prolongation of the leaf midrib.

Fig. 1036.—*Lathyrus aphaca.* Shoots showing leaves transformed into tendrils and stipules enlarged to form assimilatory organs.

Fig. 1037.—*Smilax rotundifolia.* Shoot showing tendrils formed by the splitting of the petiole rudiments.

the scales are formed from the persistent bases of foliage leaves, which become secondarily fleshy after the lamina has withered. In *Lilium* the outer scales are persistent leaf bases, but the inner scales, which in large bulbs may be very numerous, are cataphylls.

Thickened storage leaves are not necessarily only formed underground. Axillary bulbils with storage cataphylls are not uncommon on aerial shoots, as in *Dentaria bulbifera* (see Fig. 933) and *Lilium bulbiferum*, in both of which they form a means of vegetative propagation.

Fig. 1038.—*Oxalis acetosella.* Plant showing small fleshy storage leaves on the rhizome.

Neither are storage leaves confined to bulbous structures. In many species of *Oxalis*, for example, fleshy storage leaf bases are formed in clusters at intervals on the rhizomes, that is, on elongated shoots (Fig. 1038). Similar elongated groups of storage leaves are formed on the underground stems of Gesneraceae, while in the well-known root parasite, *Lathraea*, the entire shoot bears only fleshy storage leaves. Lastly, we may mention the specialized storage leaves which make up the detachable winter buds of some aquatics, such as *Hydrocharis*, which are used for vegetative propagation. These are definitely specialized cataphylls and they function almost wholly as reserve organs, not for assimilation.

Succulent plants often have fleshy leaves which store water. The normal mesophyll is replaced in such leaves by two zones of cells, one towards the upper surface, which is relatively shallow and is composed of small parenchyma cells containing chloroplasts, and another much deeper zone, making up the bulk of the leaf, which consists of very large, thin-walled cells with no chloroplasts, in which the water is held (Fig. 1039).

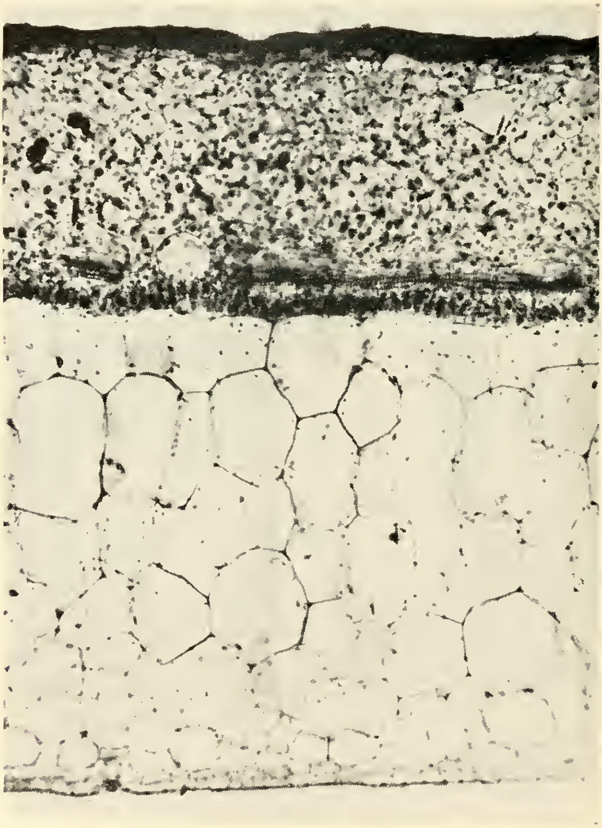


Fig. 1039.—*Peperomia* sp. Transverse section of leaf showing chlorophyll-containing tissue limited to the upper part of the lamina and large-celled water storage tissue below.

4. *Ascidial Leaves.*—These are specialized leaves in which the lamina is not flat but encloses a sac-like space (Fig. 1040). They are usually the result of overgrowth of one side of a dorsiventral leaf and may, therefore, be regarded as extreme cases of rolled leaves, or even as related to unifacial centric leaves (p. 1019). Ascidial leaves may occur as abnormalities (*e.g.*, in *Rosa*), but where they are normal developments in a species, they are almost always associated with some specialized life conditions, such as insect capture, water storage,

myrmecophily, etc., and examples of these will be dealt with in Volume IV. They are perhaps commoner among floral leaves than among foliage leaves, and in the flower they are often used as nectar containers. The "spurs" and "honey sacs" of many flowers belong to this category, and also the floral pouches of *Cypripedium* and *Calceolaria*.

5. *Buds on Leaves.*—These are exceptional occurrences and almost always associated with vegetative propagation. The buds are rarely of the bulbil type and mostly take the form of small leafy rosettes, which are usually detachable. We may classify them into two biological categories:—

Accessory buds, which are formed on the normally growing leaf blade or the petiole, either on the ventral surface, as in *Cardamine pratensis*, *Tellima*, *Drosera*, *Lycopersicum* or *Nymphaea zanzibarensis* (Fig. 1041), or on the margins as in *Bryophyllum tenuifolium*.

Fig. 1040.—*Bergenia cordifolia.* An ascidial leaf.

Fig. 1041.—*Nymphaea zanzibarensis.* Old leaf showing the development of accessory buds at the base of the lamina.

Reparative buds, which develop after separation or injury of the leaf, as in *Begonia*, *Ficus elastica* and *Bryophyllum calycinum*. They will be described further in Volume IV, under the heading of Vegetative Propagation.

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