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AN INTRODUCTION TO

STRUCTURAL BOTANY

PART I

FLOWERING PLANTS



FIG. 1. —(*Frontispiece.*) General view of a Wallflower plant (*Cheiranthus Cheiri*), about $\frac{1}{2}$ natural size. *g—g*, level of ground.

AN INTRODUCTION

TO

STRUCTURAL BOTANY

PART I

FLOWERING PLANTS

By DUKINFIELD HENRY SCOTT

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WITH 117 FIGURES IN THE TEXT AND A GLOSSARY

ELEVENTH EDITION

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PREFACE TO THE ELEVENTH EDITION

Structural Botany has now had a career of over thirty years, Part I. having first appeared in 1894, and Part II. in 1896. I have repeatedly revised the book for successive editions, but felt that the time had come when a more drastic treatment was desirable. With this end in view, I thought it wise to call in a colleague with recent experience in general botanical teaching. I was so fortunate as to secure the co-operation of my friend, Mr. F. T. Brooks, University Lecturer in Botany at Cambridge. The publishers sanctioned my proposal, and Mr. Brooks has thoroughly revised the present volume and brought it up to date.

The chief changes which he has made are in Chapter III., "Outlines of Physiology." Mr. Brooks has not only much improved the chapter as originally limited, but he has further added two entirely new sections, on Growth and on Movement of Plant Organs (pp. 233–241). Thus the physiological portion of the book, however brief, now gives a general survey of the mode of life of a typical flowering plant.

The authors are much indebted to Miss E. R. Saunders, Dr. F. F. Blackman, F.R.S., and Mr. G. E. Briggs for help kindly given.

D. H. SCOTT.

February 4, 1927.

PREFACE TO THE FIRST EDITION

THIS book is intended as a first guide to the study of the structure of plants. Botany is now taught in schools of all kinds, and wherever Botany is taught it has become customary to expect some knowledge of the construction of plants, and of the function of their organs. All that I have aimed at in this book is to secure that such knowledge, when first acquired, shall be correct as far as it goes.

My purpose has been to write an Introduction to *Structural* Botany, not a manual of Botany in general. It is absolutely necessary that schoolboys and girls, if they are to learn this science at all, should also gain a knowledge of plants in the field. For this part of the work a guide is necessary, and some such book as Professor Oliver's *Lessons in Elementary Botany* is indispensable.

The type-system has been adopted, as far as practicable, because it seems better to gain as thorough a knowledge as possible of a few plants, rather than to acquire mere scraps of information about a larger number. The types have been specially investigated for the purpose of this book, and many of

the figures are original.[1] For the rest, the authority is cited. An effort has been made to point out those structural characters which are of wide importance, as distinguished from those which are peculiar to the type, or its nearer allies.

The subject-matter is not always easy, and some parts of the book will not be followed without close attention. There is really no reason why Natural Science should be regarded in schools as a specially easy subject. If Science is to be taken seriously, it rather seems desirable that those who study it should have to use their brains as much as in learning Euclid, Algebra, or Grammar.

If any real knowledge of the subject is to be gained, practical work is essential. It is expected that the teacher should have sufficient training to be able to demonstrate to his class most of the structural features described in the book. We are now well supplied with laboratory guides, such as the works on Practical Botany by Professors Bower and Strasburger.

If the present volume is found useful, it is proposed to add a second, treating in like manner of Cryptogamic types.

I much hope that not only pupils in schools, but also private students, may derive some help from this book, and that it may awaken in some readers a genuine interest in the study of living things.

D. H. SCOTT.

February 27, 1894.

[1] Those signed "R. S." have been drawn by Mrs. D. H. Scott.

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STRUCTURAL BOTANY

INTRODUCTION

In beginning the study of plants we cannot perhaps do better than fix our attention on any common kind of plant with which we may happen to be familiar, and consider what are the most striking points in its construction. In this way we may hope, starting from the general knowledge which we all possess as the result of everyday observation, to pass on to that more accurate and systematic knowledge which is called Science.

It matters little with what plant we begin. The Wallflower is well known to everybody, so we will take that as our example.

The chief parts of which such a plant consists are easily distinguished (see Fig. 1). There is a branched colourless root, which is fixed firmly in the ground; from this rises the upright stem bearing the flat leaves. The stem is branched, each branch arising from the angle between a leaf and the main stem; the branches also bear leaves, and resemble in all

respects the stem on which they grow. Later on the flowers appear, borne on the upper part of the stem and its branches, above the leaves. These flowers, when they wither, give place to the fruits or seed-vessels, and in these the seeds themselves are ripened, which, when sown, will produce a new generation of wallflowers for next year.

Now a plant, like all living things, is made up of *organs*; thus a leaf, a stem, a root, or a flower is not merely a part of the plant, but it is a part which does some definite work for the good of the whole. The highest or most perfect plants are those in which the division of labour is most complete, in which the principle of setting apart a distinct organ for each distinct kind of work is most thoroughly carried out. The Wallflower is an example of a very highly organised plant. Later on we shall make the acquaintance of plants in which there is little or no division of labour—in which, that is, the organs are not distinct, or at least not evidently so.

The work which an organ has to do is called its *function*. In the Wallflower, as in the higher plants generally, the *root* has two manifest functions: it has to hold the plant firmly in the ground, and also to take up food from the ground. The *leaves* have for their chief office the absorption of food from the air; we shall soon find that a green plant obtains quite half its food from this source. The *stem* has to conduct the food, which the root and the leaves absorb, to other parts of the plant, and it also has to support the leaves in such a position that they may best be

able to do their work;[1] and thirdly, the stem has also to bear the *flowers*. The flowers themselves have quite a different duty to perform. Their business is to produce the *seeds*, and so to provide a supply of new wallflowers for the future. We see, then, that the organs which we have mentioned are of two kinds. On the one hand, the root, stem, and leaves do work for the benefit of the particular plant to which they belong; these we call the *vegetative organs*. On the other hand, the flowers are concerned in the production of fresh plants; they are therefore called the *reproductive organs*.

One important division of Botany, then, is concerned with such questions as those which we have just roughly indicated. We aim at finding out how a plant lives, what different kinds of work it has to do in order to live and to produce others of its kind, and by means of what organs the work is done; also what is the structure of these organs by which they are enabled to perform their office. All these questions belong to *Physiology* in its widest sense. Physiology is concerned with the question what a plant *does*, and what its various organs do. The answer to such questions must be obtained by *experiment*. The study of structure, or *Anatomy*, is from this point of view a necessary auxiliary to physiology.

But we can also look at plants from a different point of view. Suppose, for example, that instead of considering the Wallflower alone, we compare it

[1] It is often convenient to speak of the stem and leaves together as *the shoot*.

with some other plant, such as a Potato. A potato plant differs in many points from the Wallflower, but

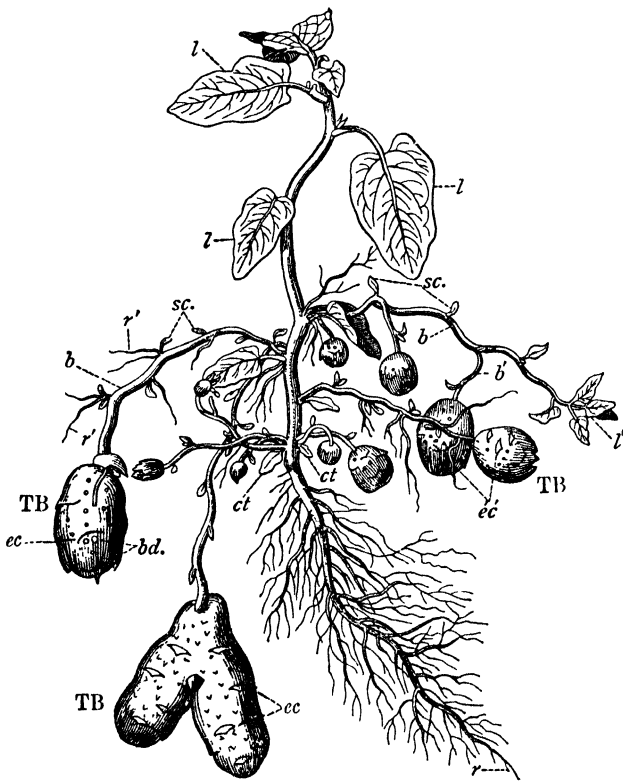


FIG. 2.—Young Potato plant (reduced), raised from seed. *ct*, the first leaves, or *cotyledons*; *l*, the foliage-leaves; *b*, *b'*, branches, bearing the tubers; *sc*, scale-leaves; *r*, *r'*, roots; TB, tubers; *ec*, their scale-leaves; *bd*, their buds. (From Sachs, after Duchartre.)

we will confine ourselves to one of these differences.

It not only consists of the stem bearing its green leaves and ultimately producing the white or mauve flowers, and of the root with its fibrous branches, but it also forms the potatoes themselves (or *tubers*, as they are called), which we eat. Now these potatoes, as every one knows, grow, like the root, underground, borne on subterranean branches. Both they and the branches which bear them are colourless, and from their general appearance and position every one who has not learnt Botany at once classes them as roots. But is this their true nature?

If we closely examine the branches on which the potatoes grow, we shall find that they bear small scaly leaves (Fig. 2, *sc*). Similar little leaves (*ec*) will be found on the potato itself, adjoining the "eyes," and the "eyes" themselves are buds (*bd*), which grow out into new plants when the potatoes are sown. Leaves and buds, however, are characteristics of stems; the former are never, the latter rarely, found on undoubted roots. Besides this, a more thorough examination would show that the internal structure and the mode of growth of the potatoes and of the underground branches which produce them are those of stems and not of roots. Further, we may sometimes find on the parts of the potato plant above the ground bodies which are intermediate in form and structure between potato tubers and ordinary green branches. For these reasons, all botanists are agreed in regarding potatoes, in spite of their appearance and underground position, as forming part of the shoot and not of the root. In other words, we come to the conclusion that

certain shoots of the potato plant have become completely modified, so as to lose all the more obvious characters of shoots, and to bear a superficial resemblance to roots. These changes are the external manifestation of a complete alteration of function. The potato tubers have given up the usual functions of shoots, and become adapted to serve as storehouses of food (chiefly starch) for the young plants which will grow from the "eyes" next year.

If, then, we compare the potato plant with the Wallflower, we find that, while in the latter the shoot consists entirely of above-ground branches bearing green leaves, in the potato plant certain parts of the shoot are changed into underground colourless organs, bearing scale-leaves, and ending in tuberous swellings, which are storehouses of food.

But we must not suppose that all underground organs which serve this purpose are shoots. Turnips, radishes, and dahlia tubers are also underground parts of plants, and in function are similar to potato tubers, but here the structure and mode of growth show that we have to do with modified parts of the root (Figs. 3 and 4).

The comparison of various plants thus shows us that quite different parts may be changed, so as to serve the same function, and that the same part may be modified to perform quite different functions. We shall meet with plenty of examples of this later on, but the instances just given will suffice to introduce us to the second great division of the science of Botany, namely, the *Morphology* of plants. This is

based upon the comparative method of study as applied to plants and their organs.

To put the distinction shortly, while, as we have seen, physiology asks the question what each part of a plant *does*, morphology inquires what it *is*. The word "morphology" means the "study of form," but this literal meaning, as so often happens with scientific terms, gives a very imperfect idea of what is really implied. External form, at any rate, is quite an



FIG. 3.—Conical root of Bryony. Reduced. (After Balfour.)

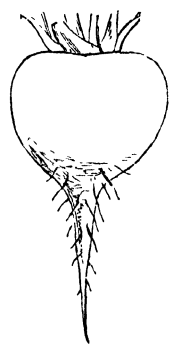


FIG. 4. — Fleshy root of Turnip. Reduced. (After Balfour.)

insignificant part of the subject of morphology, which is much more concerned with internal structure, relative position of parts, and the changes which they undergo during development. By the accurate comparison of plants in all these respects, morphology aims at finding out the relationships between them—

that is, it endeavours to construct a natural classification of the vegetable kingdom. Classification is often treated as a separate part of the science, called Systematic Botany, and this is a convenient division, but Systematic Botany can only be satisfactorily based on the comparative study of plants—that is, on morphology.

While it is easy to distinguish sharply between the physiology and morphology of plants, it is more important to remember that neither can be pursued to any advantage without the other. Physiology without morphology would teach us much about the life of individual plants, but could give us no idea of the vegetable kingdom as a whole, or of the relationship between the innumerable species of which it is composed. Morphology without physiology, on the other hand, would be just as barren, for the complex modifications of the organs of plants would be wholly unintelligible without reference to the functions to which they are adapted. Only by examining plants from both points of view can we attain to any knowledge of them which deserves the name of science.

The method pursued in this book is to take in succession a series of types representing important groups of plants, to examine each of them as fully as our space permits, with reference to both structure and function, and to compare them together. It will often be necessary to supplement the study of our main types by that of other plants which resemble them on the whole, but better illustrate some particular

point, for Nature does not provide us with perfect types ready made.

In this way we may hope to gain some real knowledge of a few plants, which may serve as a firm foundation for more extended study afterwards. In choosing the order of our types, we will begin with the more highly organised plants, in which the division of labour among the organs is most complete. We do this, partly because the higher plants are most familiar to us in everyday life, and partly because we shall gain from them the clearest conceptions of organs and their functions.

Besides morphology and physiology, there are some more divisions of Botany which we must mention. One of these is the study of *fossil* plants—that is, of the vegetable remains which have come down to us preserved in the earth from ages long past. This is called the *Palæontology* of plants, or sometimes *Palæo-botany*—that is, the science of ancient plants. From one point of view this is simply a part of morphology; we compare the fossil plants among themselves and with recent ones, and draw conclusions, so far as we are able, as to their relationships. We cannot study their physiology, for they are dead; we may, however, draw some inferences as to their mode of life from their structure. So far, palæontology is concerned with the same questions as recent Botany, but we also have to learn the succession of the strata in which the fossils are found, and so to trace their relative geological age, or, in other words, their distribution in time. Inquiries of this kind are peculiar to

palæontology, and are of the greatest possible importance, because they enable us to a certain extent to trace the past history of the different kinds of plants. To take only one example: the enormously rich vegetation which is so well preserved in the coal-measures consisted of forms of plants which have long since become extinct. The classes to which many of the great trees

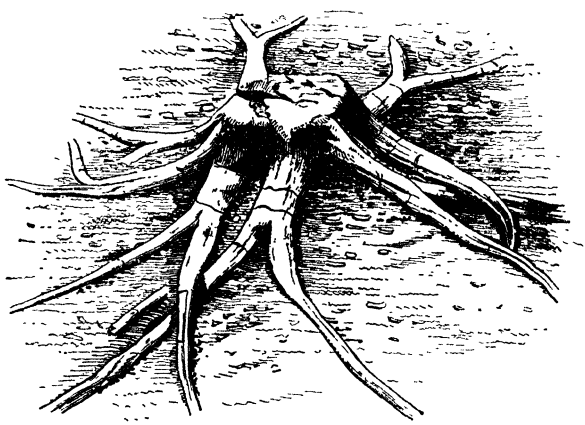


FIG. 5.—Stump and roots of a Fossil Tree (*Stigmaria ficoides*) from the carboniferous sandstone. The diameter of the stump is 4 ft. 4 in., and the spread of the roots 28–30 ft. (After Williamson.)

of that period belonged (such as the *Stigmaria* figured) are now only represented by a few small herbaceous plants (such as *Selaginella*).[1] On the other hand, most of the groups which are now of the greatest importance had not then appeared, and their first representatives are found in much later rocks.[2] This part of the science, however,

[1] See Part II., *Flowerless Plants*, p. 1.

[2] See Juke's *School Manual of Geology*, p. 280.

cannot be further touched on here. We shall only be able to concern ourselves with plants now living.[1]

Then we have *Geographical Botany*, from which we learn the parts of the world in which the different kinds of plants grow wild, or, in other words, their distribution in space. This teaches us, for example, the very uniform character of alpine vegetation in all parts of the world; the peculiarities of the Flora[2] of oceanic islands, deserts, and so on. This also leads to very important conclusions, especially when we study the geological and climatic changes which have influenced the present distribution of plants. We shall call attention to the distribution of our various types, but this part of Botany cannot be pursued far without a much wider knowledge of plants than is aimed at in this book.

A rather new branch of Botany, or at least one which is being pursued very actively at the present time, is called *Ecology* (οἶκος, "a house"), and is concerned with the study of the plant *at home*, that is, in relation to its surroundings. Ecology aims, for example, at finding out why some plants grow in woods, others in marshes, others on sand-dunes; how plants are affected by one another or by animal neighbours; the causes of their succession according to the seasons; and so on. Ecology has a great deal to do with Geographical Botany, because it helps to explain the distribution of plants, and with Physiology, because one must know how a plant lives in order to understand its relation to its surroundings.

After these introductory considerations, we will now go on at once to our first type.

[1] Scott, *Studies in Fossil Botany*, 3rd edition, vols. i. and ii., 1920 and 1923.

[2] By the *Flora* of a country we mean all the plants which grow wild there, collectively.

CHAPTER I

TYPE I

THE WALLFLOWER (*Cheiranthus Cheiri*, L.[1])

I. *EXTERNAL CHARACTERS*

A. VEGETATIVE ORGANS

a. The Shoot

THE Wallflower, a native of Southern and Central Europe, is occasionally found naturalised in England, and derives its name from growing commonly on old walls. It is a *perennial*—that is to say, it lives for a number of years. It does not die down in winter, nor does it lose its leaves in autumn. The leaves, however, gradually drop off from the older parts of the stem.

The stem is erect and branched (see Fig. 1), and its lower part is covered by scales of pale brown bark. This part is hard and woody. The upper portions, both of the main stem and branches, are softer and coloured green, and are rather hairy. The surface of the stem is ridged lengthways, the ridges being more conspicuous on the younger parts. The ridges are

[1] The letter *L* is the initial of the author (Linnæus) from whom the plant received its present name.

generally five in number; each of them runs vertically along the whole length of the stem or branch, and passes through the places where the leaves are inserted. The ridges are most prominent just below the insertion of the leaves.

Both in the main stem and its branches it is evident that the lower parts are the older. For some distance above the ground there are no leaves; they have dropped off, and we only find the scars which they have left. Then we come to leaves which are beginning to wither; a little higher up they are green and fresh, and of full size. Higher up still we find them smaller and more delicate, while at the top of each branch the leaves are only just forming, and we can trace them up to the extreme tip, until they are so small that we can no longer distinguish them. We see, then, that the formation of new organs goes on from below upwards, or, in other words, the growth takes place at the apex of the branch. The extreme end of the branch, where the young leaves are just making their appearance is called the *growing-point*. The growing-point with the young leaves which surround it is called the *leaf-bud*.

The branches do not arise indiscriminately on any part of the stem, but every branch grows from the angle between leaf and stem, just above the insertion of the leaf. This angle is called the *axil*, and the branches are said to be *axillary*. The main stem continues its growth indefinitely in the same direction, giving off its branches laterally.

The arrangement of the leaves on the stem requires

rather close attention to make out. We see at once that no two leaves arise at the same level. Every leaf is placed a little above or below its next neighbours. The leaves, therefore, are said to be *alternate.*

We find further that they are arranged in a spiral. An imaginary line connecting the bases of the successive leaves together, would wind upwards round the stem, just like the thread of a screw; here, however, the spiral ascends from the right up to the left, like a left-handed screw, in the reverse direction to an ordinary right-handed one.[1] Now, if we count the leaves carefully, beginning from below, and *not* counting the leaf taken as our starting-point, we shall find that the *fifth* leaf comes exactly above the one we started with, and in order to reach this fifth leaf we have had to follow the spiral exactly twice round the stem. The ridges make it much easier to see which leaves come in the same straight line; for, as we saw just now, each ridge runs straight from one leaf to that vertically above or below it. This arrangement of the leaves may be expressed by the fraction $\frac{2}{5}$, in which the denominator indicates the number of the leaf which comes directly above the starting-point, while the numerator tells us how many times the spiral line travels round the stem before the fifth leaf is reached. This fraction $\frac{2}{5}$ also expresses the *divergence* or angle between two successive leaves, which is equal to $\frac{2}{5}$ of the circumference of the stem. The way in which leaves are arranged on the stem is called *phyllotaxis,* and varies very much in different kinds of plants.

[1] In the diagram (Fig. 6) the spiral ascends from left to right.

The whole length of the stem is divided into *nodes* and *internodes*. The part where a leaf is borne is called a *node*, the spaces between the leaves are the *internodes*.

Each leaf is attached to the stem by a narrow base. It has no distinct stalk, but the blade of the

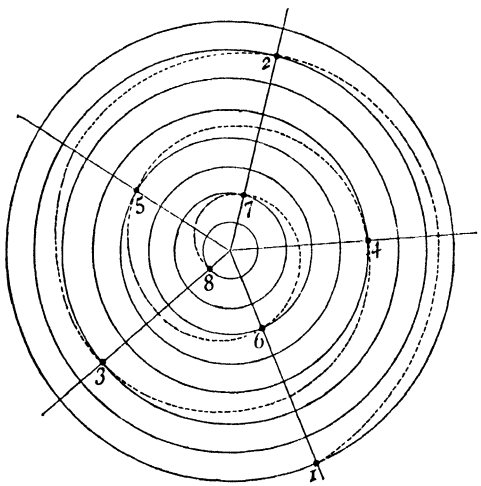


FIG. 6.—Diagram to illustrate $\frac{3}{8}$ Phyllotaxis. The dotted line represents the leaf-spiral, which is seen in horizontal plan, the centre corresponding to the apex. The concentric circles represent the successive nodes. (After Van Tieghem.)

leaf is very narrow near the base, and broadens out quite gradually for about two-thirds of the whole length, and then narrows again rather more rapidly to the pointed end. The leaf is technically called *sessile*, because the blade is seated on the stem directly, without the intervention of a leaf-stalk or petiole, such

as we see in the leaf of a Vine or Geranium. The narrow part of the blade, however, only differs from a leaf-stalk in being slightly winged. The part of the leaf where it joins the stem is called the *leaf-base*; this remains in connection with the stem after the rest of the leaf has dropped off.

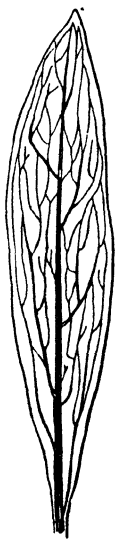


FIG. 7.—Leaf of Wall-flower, natural size, showing the chief veins. (R. S.)

The shape of this leaf is expressed in botanical language by the words *lanceolate*, *acute*, and *entire*. The word *lanceolate* refers to the general outline, which is like that of a lance-head; the word *acute* indicates the pointed apex; while the term *entire* means that the edge is not toothed or divided in any way.

The upper surface of the leaf is dark green and very slightly hairy. The under surface is of a lighter green, and has many more hairs. The hairs are closely applied to the surface, and cannot be seen well without a lens, though they can easily be felt.

The leaf is traversed from end to end by a stout midrib, or principal *vein*, which is more prominent on the lower surface, and gradually tapers towards the apex. From the midrib branch-veins are given off at irregular intervals, which turn upwards so as to run nearly parallel to the midrib. These main branches

join on to each other, and themselves give off innumerable lesser branches, which permeate every part of the leaf, and are united among themselves into a fine network. The finest branches of all, however, end blindly within the meshes of the network. The smaller veins can only be traced with the help of a lens (see below, p. 65, Fig. 24).

We have now described the chief external characters of the stem and leaves. To complete our sketch of the vegetative organs, we will next consider the root.

b. The Root

If we pull up a Wallflower and wash away the earth which clings to the root, we find that this, like the stem, has a main axis, which grows straight downwards, in the same line with the erect axis of the stem. A main root of this kind is called a *tap-root*. Of course the root meets with more resistance to its growth than a stem does, and sometimes it is forced to diverge more or less from its vertically downward direction (see Fig. 1). From the tap-root a number of branches are given off. These branches do not grow straight down, but take an obliquely descending course, forming an angle a little less than a right angle with the tap-root. From these principal branches other much smaller ones arise, and these also ramify repeatedly. The finer branches of the root do not take a fixed course, but penetrate the soil in all directions equally. If the plant has been very carefully taken up, we shall find that particles of earth stick firmly to the very youngest branches of the root

a little above their extreme tips. This is because these parts of the root are clothed with very fine *root-hairs* (see Fig. 29, p. 77), which have withered away from the older parts. These *root-hairs* are barely visible to the naked eye, and must by no means be confused with the *rootlets* or fibres already described, to which they bear no resemblance in structure, as we shall find when we come to the microscopic work. Each growing-point of the root and its branches is covered by a *root-cap* (see below, pp. 78 and 86). We notice as conspicuous differences between the root and the shoot, that the former bears no leaves and is not green in any part.

We shall find a young seedling more convenient for studying the root than an older plant. On such a seedling it is possible to make out that the branches of the tap-root are not arranged irregularly, but form four vertical rows.

B. Reproductive Organs

a. The Flowers

The branches which bear the flowers do not at first differ in any way from ordinary vegetative branches. They arise in the axils of leaves, and for some time bear leaves themselves in the usual way. But soon the production of leaves ceases, and from that time onwards the branch bears flowers only. Each flower may itself be regarded as a modified branch (borne on the main branch), the leaves of which differ greatly in arrangement, form, structure, and colour from the

vegetative leaves. The flowers, unlike the ordinary branches, do not arise in the axils of leaves, for there are no leaves at all on the part of the plant which bears them. This is characteristic of the Wallflower and its relations. In most plants the flowers, like other branches, are borne in the axils of leaves.

The entire group of flowers borne upon the stem is called the *inflorescence*. In the Wallflower the flowers are borne laterally on a main axis, and are

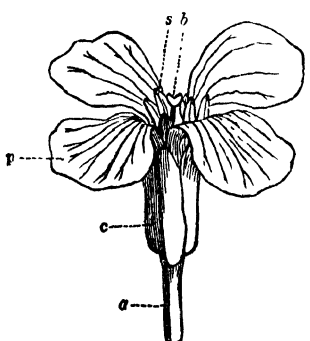


FIG. 8.—Flower of Wallflower. *a*, flower-stalk; *c*, calyx; *p*, corolla; *s*, stamens; *b*, stigma. (After Balfour.)

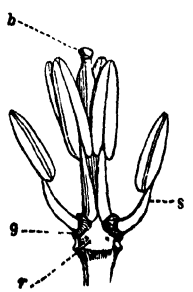


FIG. 9.—Same flower, with calyx and corolla removed. *s*, stamens; *b*, stigma at top of pistil; *r*, receptacle; *g*, honey-glands at base of short stamens. (After Balfour.)

stalked. The main axis terminates in a bud which is continually forming new flowers as long as growth continues. Thus the oldest flowers are at the bottom, and the youngest at the top. An inflorescence of this kind is said to be *indefinite*. An indefinite inflorescence with a single elongated main axis and stalked flowers is a *raceme*.

Now we will consider the parts of a single flower in detail. The first point that strikes us is that, while the stalk (*pedicel*) is quite bare, all the leaves are crowded together at the end of the branch. The floral

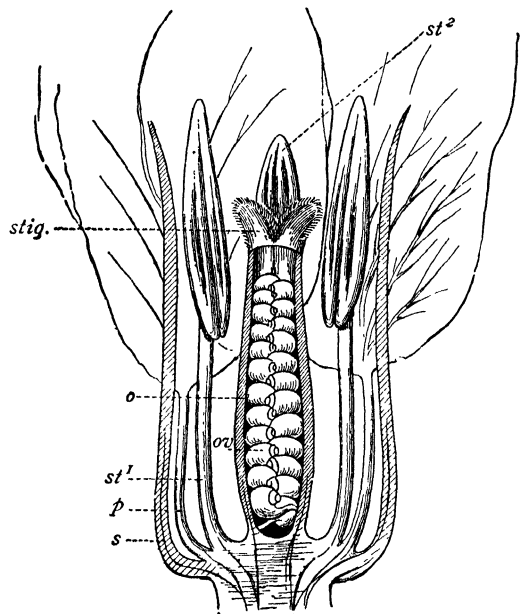


FIG. 10.—Diagrammatic view of the flower of Wallflower (enlarged) in longitudinal section, cut in median plane of outer sepals. *s*, sepal; *p*, petal; st^1, two of the long stamens; st^2, one of the two short stamens; *o*, ovary; *ov*, ovules; *stig*, stigma. (R. S.)

leaves are not arranged spirally, but two or more grow at the same level. The enlarged end of the stalk, on which the floral organs grow, is the *receptacle*, or *thalamus*.

Beginning at the outside of the flower, we first come

to four small narrow leaves of a purplish colour (see Fig. 8, *c*). These leaves are not all inserted at the same level. They are in two pairs, placed at right angles to

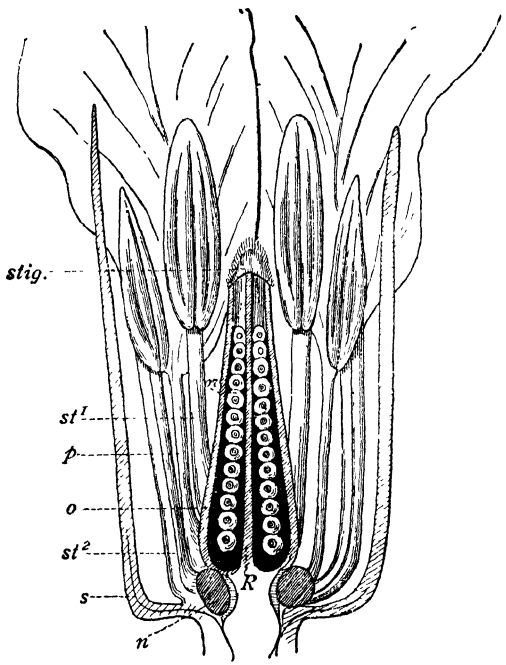


Fig. 11.—Diagrammatic view of the flower of Wallflower (enlarged) in longitudinal section, passing through median plane of inner sepals. *s*, sepal; *p*, petal; st^1, long stamens; st^2, short stamens; *o*, ovary; *ov*, ovules; *stig*, stigma; *n*, nectaries at base of short stamens; *R*, septum between the two carpels. (R. S.)

each other, and one pair is inserted rather farther in than the other pair (see Figs. 12 and 13). This is seen very clearly in the bud (Fig. 12), though less easily

in the open flower. Each of these four leaves is called a *sepal*, and collectively they form the *calyx*; as the sepals are not joined together, the calyx is said to be *polysepalous*.

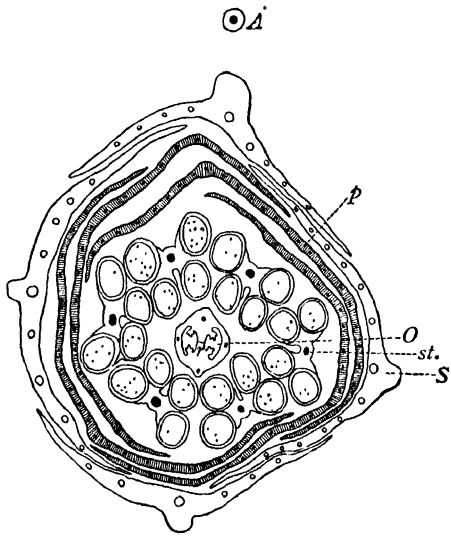


FIG. 12.—Transverse section through a flower-bud. *A*, position of axis of inflorescence; *S*, sepals (four in number); *p*, petals (shaded) (four in number); *st*, stamens (six in number, each with four pollen-sacs); *O*, ovary (of two carpels). Compare the diagram, Fig. 13. Magnified about 12 times. (R. S.)

The diagram, Fig. 13, represents as it were the ground plan of a flower, and shows the relative position of all its parts. In order to fix this, it is necessary to know how the flower is placed with reference to the axis of the inflorescence. This axis is indicated by a dot in the diagram. It will be seen that the two outer

sepals are so placed that one lies next the axis (*posterior*), and the other remote from it (*anterior*). The two inner sepals are placed at the sides (*laterally*), alternating with the outer two. The two inner sepals are bulged out at the base; we shall see the reason for this directly. In the bud before it opens, the calyx completely encloses all the other parts of the flower.

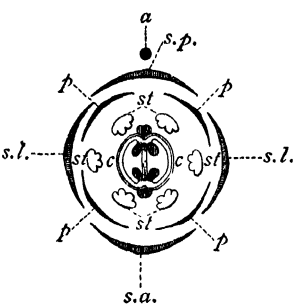


FIG. 13. — Floral diagram, or ground plan of the flower of *Cheiranthus*. *a*, axis of inflorescence; *s.p*, posterior sepal; *s.a*, anterior sepal; *s.l*, lateral sepals; *p*, the four petals; *st*, the six stamens (the four long ones are shown connected in pairs); *c*, the two united carpels, forming the pistil.

Inside the calyx we find four floral leaves forming a single ring, or *whorl*. These are the *petals*, the most conspicuous part of the flower. In the wild Wallflower they are yellow; in cultivated specimens they are generally more or less brown. Each petal is broad and rounded above, and tapers into a narrow stalk below (see Figs. 10 and 11). The four petals form collectively the *corolla*, which is here said to be *polypetalous*, because the petals are not connected together. The petals are so placed as to alternate with the four sepals—that is to say, the middle of each petal comes exactly opposite the space between two sepals (see Figs. 12 and 13).

Both the sepals and the petals are veined, but not in such a complicated way as the vegetative leaves.

So far the organs of the flower have borne an obvious resemblance to ordinary leaves. The next whorl is very different, and consists of bodies which, so far as their outward form is concerned, are not at all leaf-like. Each consists of a longish stalk, bearing at the top a little boat-shaped case of a yellowish colour. These are the *stamens* (see Figs. 8, 9, 10, and 11). There are six of them, four of which are longer than the other two. The two shorter stamens stand on either side of the flower, and each of them is placed just between two of the petals, and just opposite the two inner lateral sepals. The four longer stamens are placed rather farther in, so that all six stamens might be regarded as forming *two* whorls. The longer ones are in two pairs, each pair standing between two petals, and just opposite the two outer (posterior and anterior) sepals. (See Fig. 12 and diagram, Fig. 13.)

The stalk of the stamen is called the *filament*; the body at the top of the filament is the *anther*. The filament is continued up through the middle of the anther, and is here called the *connective*, because it connects together the two halves (*lobes*) of the anther. When ripe, the anther bursts to discharge a yellow powdery substance called *pollen*.

Just inside the bases of the two shorter stamens are two large green honey-glands (*nectaries*). The filaments are bent outwards to make room for them, and this causes the bulging of the adjacent lateral sepals, which we noticed in examining the calyx (see Figs. 9 and 11).

The middle of the flower is occupied by the *pistil* This is a nearly cylindrical hollow body, green in colour, tapering a little towards the top, and surmounted by a forked outgrowth. The lower thicker part, which occupies more than three-quarters of the whole length, is the *ovary*, and the forked outgrowth at the top of all is the *stigma*, while the short tapering portion which connects the two is the *style* (see Figs. 9, 10, and 11).

The hollow ovary is divided lengthways into two compartments by a membrane called the *septum*. This membrane marks the boundary between the two[1] *carpels*, the name given to the floral leaves of which the pistil is composed. We see, then, that the two carpels are so placed as to lie opposite the two inner lateral sepals. Within the ovary are the young seeds, or *ovules*, as they are called at this early stage. They grow on the walls of the ovary adjoining the septum. As, however, we are only dealing with external characters at present, we will postpone any further examination of the interior of the ovary and of the ovules (see p. 104).

The ovules only develop into the seeds after fertilisation, which is brought about by the pollen. In order that the ovules may become ripe seeds, which can grow into young plants, it is necessary that the pollen should come into contact with the

[1] E. R. Saunders, who has recently investigated the morphology of the ovary in detail, considers that there are four carpels in the ovary of the wallflower, two of which are sterile and form the valves, the other two being fertile and forming the septum (see Fig. 50, p. 138).

stigma of the pistil. The whole process of fertilisation will be described later on, when we have made ourselves acquainted with the internal structure of the floral organs (see p. 122).

b. The Fruit

The *fruit* is the ripened pistil, and contains the *seeds*, which are the fertilised ovules. It continues to show the same general structure as the pistil, but grows much larger, and undergoes some important changes, a description of which will be found on p. 137. During the development of the pistil into the fruit all the other floral organs—calyx, corolla, and stamens—drop off.

II. *INTERNAL STRUCTURE*

A. The Cells

If we examine under the microscope a thin slice, or section as it is called, from any part of an ordinary plant, say, for example, a section cut straight across the stem of a Wallflower, we find that its substance is not uniform, but is divided up by a network of walls into innumerable minute chambers of varying size and shape (see Fig. 20, p. 48). If we make another section at right angles to the first, say a section lengthways through the stem, we find the same structure, except that in this view the chambers appear to have somewhat different shapes (see Fig. 22, p. 52). Combining the two views together, we come to the conclusion that the whole substance of the plant is composed of a system of closed compartments. This is the reason why, if a juicy fruit like the melon is cut into pieces, all the juice

does not run out, but only a little is lost. The juice is contained in these little closed chambers, which hold it fast, and only those which are actually opened by the knife are emptied (see, however, p. 40).

Now these chambers, of which the whole substance of almost all plants consists, are called *cells*. They are nearly always so small that they cannot be distinguished at all except under the microscope. Few reach a diameter of $\frac{1}{100}$ of an inch, while many measure only $\frac{1}{1000}$ of an inch, or less. The fact that plants have a cellular structure is far from being a modern discovery. Cells were discovered in plants by Robert Hooke[1] in 1667, and within the succeeding fifteen years the internal structure of many plants was worked out by Nehemiah Grew in England, and Marcello Malpighi in Italy. The early anatomists were struck by the similarity of many vegetable tissues to the honeycomb of a bee, and they applied the word "cell" to the chambers in both cases in the same sense.

From the time of Grew and Malpighi onwards until well within the nineteenth century—for a period, that is, of quite a century and a half—those botanists who troubled themselves at all about internal structure attended chiefly to the walls of the cells. These are much the most conspicuous features in the section

[1] See his *Micrographia; or, Some Physiological Descriptions of Minute Bodies made by Magnifying Glasses, with Observations and Enquiries thereupon* (London, 1667), especially chapter xviii., "Of the Schematisme or Texture of Cork, and of the Cells and Pores of some other such frothy Bodies."

through any fully formed organ, when seen under the microscope. The network of walls enclosing the cavities strikes the eye at once. We do not at first particularly notice the contents of the cavities, but the research of the last century has shown that it is the cell-contents, after all, which are the most important part of the cell; it is the contents which form the wall, not *vice versâ*, and in many plants the cell-contents escape, and are then quite able to grow and increase without any wall at all, while the cell-wall without its contents is a dead shell, incapable of growth or activity of any kind.

a. General Structure of the Cell

We will now shortly consider the structure of a single cell, and we will begin by describing one from quite a young part of a plant, such for example as the bud at the growing end of a branch.

A young cell (see Fig. 14, *A*), like one of those of which a growing-point is formed, is surrounded on the outside by a delicate but firm and elastic *membrane*, the *cell-wall*, by which it is separated from its neighbours. The wall consists chiefly of a substance called *cellulose*, which is chemically very similar to starch, and is composed of the same chemical elements (carbon, hydrogen, and oxygen) in the same proportions.[1]

The strength and elasticity of all parts of the plant are ultimately due to the cell-walls, which serve as a firm supporting framework for the whole structure. In such young parts as we are now considering, how-

[1] The formula is $(C_6H_{10}O_5)_n$.

ever, the cell-walls are still very thin, and for this reason growing-points are very delicate, and require external protection, which in the case of stems is afforded by the surrounding leaves.

The interior of the cell is almost completely filled by a soft, viscid, finely granular, colloidal substance, the *protoplasm*. The outer part of the protoplasm, where it borders on the cell-wall, is clearer—that is, more free from granules—than the rest. The protoplasm consists of a mixture of various substances, called by chemists *proteins*, which are more or less similar in composition to albumen or white of egg. These are very complicated bodies, not yet fully investigated by chemists; they are composed of the elements, carbon, hydrogen, oxygen, nitrogen, and sometimes also sulphur and phosphorus. Besides the proteins, active protoplasm always contains a large proportion of water. Physically it resembles a very thick fluid, but it has powers of spontaneous movement and continuous changes of form such as no other fluid in nature possesses.[1] Protoplasm is found in all cells without exception in which growth is going on, or in which food is assimilated, or any new structure formed, or any kind of spontaneous movement carried out. It is, in fact, the seat of all those processes (whether in plants or animals) which distinguish living organisms from lifeless matter. The word "protoplasm," meaning that which is *first formed*, was invented by the Bohemian physiologist Purkinje

[1] No part of the Wallflower plant is convenient for observing these movements of protoplasm, so some special illustrations of them from other plants will be given below (see p. 41).

in 1840, and was used independently by the German botanist von Mohl in 1846, to express the fact that this substance is the primary part of the cell, while the cell-wall is a secondary product derived from it.

Embedded in the protoplasm is a roundish denser body, which has a more coarsely granular appearance

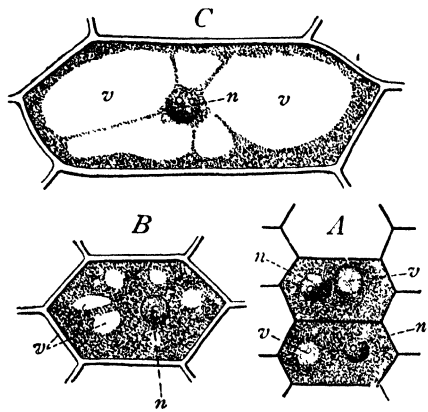


FIG. 14.—Young cells at various stages of growth. *A*, Very early stage; the cell-walls are quite thin, and the protoplasm almost fills the cell. *B*, Rather older cell, cell-wall thicker, and vacuoles more numerous. *C*, Older still; the greater part of the cavity now forms a large vacuole. *n*, nucleus; *v*, vacuoles. (After Van Tieghem.) Magnified several hundred times.

than the rest of the protoplasm. This body is the *nucleus*. A nucleus is certainly present in all living cells of the higher plants, and also in the great majority of those of the lower plants. In very young cells it is of relatively large size, and its diameter may be more than half that of the entire cell. Its complicated structure cannot be fully described here, but it may be mentioned that in

many cases the apparent granules are found, under a sufficiently high power of the microscope, to represent extremely minute threads or fibrils. The nucleus also contains one or more comparatively large rounded masses distinct from the fibrils, and called the *nucleoli* (see Fig. 17, p. 39). The nucleus has a definite membrane. The substance of the nucleus consists of various chemical bodies which are similar to, but not altogether identical with, those of which the rest of the protoplasm is built up; a complex compound containing phosphorus appears to be constantly present in the nucleus. The protoplasm excluding the nucleus is now generally called *cytoplasm*.

Most cells contain only one nucleus, but in very long cells a number of nuclei are often found.

The cytoplasm, nucleus, and cell-wall are the most constant constituents of a vegetable cell. The cytoplasm, as we have seen, is absolutely constant in all living cells without exception; the nucleus is equally general in the higher plants, though in some of the lower ones its presence has not been proved; the cell-wall is formed sooner or later in all cells of the higher plants, but is very frequently absent, at any rate for long periods, from certain cells of the simpler plants.[1]

If we examine rather older cells, such as those which we find at a little distance below the growing point, we shall see that the whole cell is larger, and that its cavity is no longer so nearly filled by the cytoplasm (Fig. 14, *B*). Clear spaces, which had already appeared in the cytoplasm at an earlier stage (*v* in the figures), have now increased in number; they are filled with

[1] See Part II., *Flowerless Plants*.

water containing various organic and inorganic substances (salts, sugars, acids, etc.) in solution, and called the *cell-sap*. The spaces filled with cell-sap are known as the *vacuoles*, because they look as if they were empty.

The nucleus increases little in size, and now bears a much smaller proportion to the whole cell than it did at first. The cell-wall will have become somewhat thicker (see Fig. 14, *B* and *C*).

A full-grown but still living cell, such as we might find in the older parts of the Wallflower, has its cytoplasm reduced to a thin layer, lining the inside of the wall. The whole interior of the cell appears empty—that is, it is occupied by one large vacuole containing cell-sap. This has been formed by the smaller vacuoles running together. The layer of cytoplasm lining the cell-wall is often called the *primordial utricle*. The nucleus has undergone little change, but is now placed close against the wall, embedded in the cytoplasmic layer which lines it. The cell-wall itself has been further thickened by the deposit of new cellulose from the cytoplasm.

This is the structure of most mature living cells of plants. The protoplasm does not keep pace with the growth of the whole cell; it may even actually diminish in amount, owing to its being used up to make new cell-wall and for other purposes, quicker than it is renewed by taking in food. Some cells lose their protoplasm altogether; then they are dead, and incapable of any further growth, though they may still be of use to the plant as passages for sap or as a mechanical support. We shall find plenty of examples of altered cells of this kind in various organs of such plants as the Wallflower, more especially in the wood.

b. Special Contents of Cells

Many other structures are found in cells besides cytoplasm, nucleus, and cell-wall. Some of these we will not trouble about until we come to them in describing the internal structure of our types. One or two, however, are so important that they must be mentioned at once.

α. Chlorophyll-Granules or Chloroplasts

If we examine, under the microscope, a living cell from the green succulent parts of the leaf or stem, we shall find, embedded in the cytoplasm, a number of round bodies of a bright green colour (see Figs. 19, p. 42, and 26, p. 69). If we soak the leaf or stem in alcohol, and then examine its cells, we shall find that the green colour has gone, the colouring matter having been dissolved by the alcohol, which becomes of a dark green tint in consequence. The round bodies themselves remain, however, unaltered in size and shape, though now colourless. The green colouring matter is *chlorophyll*,[1] the round granules which contain it are the *chlorophyll granules* or *corpuscles*. Cytoplasmic granules of this kind are called *plastids*. The chlorophyll granules consist of cytoplasm, rather denser and firmer than the ordinary cytoplasm of the

[1] The solution obtained by soaking a green leaf with alcohol contains actually a number of distinct pigments the exact chemical composition of which is known. Two of these pigments are green (*chlorophyll a* and *chlorophyll b*), and two are yellow (*xanthophyll* and *carotin*). Carbon assimilation (photosynthesis) cannot take place without the green pigments. It will be convenient in this book, however, to use the term chlorophyll to denote all these pigments collectively.

cell, and saturated by the green colouring matter. All green parts of plants owe their colour to the presence of chlorophyll-corpuscles in their cells.

We have said above that one of the two main functions of the shoot is to take up food from the air. The great food-substance which green plants obtain from the air is *carbon*. About half the solid substance of plants consists of this element, which enters into all the chemical compounds of which living things are built up. The whole of this carbon is obtained by ordinary green plants from the carbon dioxide (CO_2), which is contained in small quantities in the air. In ordinary air the amount of this gas is equal to about three parts in ten thousand. The carbon dioxide is decomposed, the oxygen given off again, and the carbon retained, to help in forming the various organic substances of the plant.[1] Now this decomposition of carbon dioxide is entirely performed by the chlorophyll granules, and they can only do this work under the influence of *light*. We see, then, that the chlorophyll granules are of the greatest possible importance to the plant, for they are the organs by which alone, with the help of the sun's rays, it can obtain its carbonaceous food from the air. Both parts of the granule are necessary for the process; the chlorophyll itself is useless without the cytoplasm of the granule, and the cytoplasm is quite unable to do the work unless it contains chlorophyll. The process of nutrition just

[1] In all probability only half the oxygen of the CO_2 is given off, the other half of the evolved oxygen being derived from the simultaneous decomposition of H_2O.

described is known as *assimilation*, or, more accurately, as *carbon*-assimilation or *photosynthesis*, for assimilation is sometimes used in a wider sense. To this process the formation of all organic substances whatsoever is ultimately due, and carbon-assimilation by green plants may thus be fairly regarded as the most fundamentally important of all physiological processes. The assimilation of carbon is not really so simple a matter as might appear from the rough sketch just given; we shall return to the subject later on, when we come to the special consideration of physiological questions (see Chapter III.).

β. *Starch Granules*

Another important body very generally, though not always, found in the cell-contents is *starch*. Starch contains the three elements, carbon, hydrogen, and oxygen in the proportion $C_6H_{10}O_5$, but the molecular weight is much larger than is indicated by this empirical formula. It occurs in the form of granules, which are easily identified under the microscope on treating with iodine, which gives them a deep blue colour. The larger granules show *stratification* (see Fig. 15, *A* and *C*); that is to say, the substance

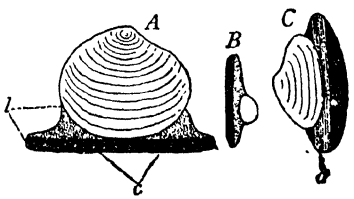


FIG. 15.—Starch granules, and leucoplastids. From an orchid (*Phajus*). *A*, large granule, showing stratification; *l*, the leucoplastid; *c*, protein crystalloid; the hilum is at the opposite side of the granule, near the letter *A*. *B*, Very young granule, still much smaller than the leucoplast. *C*, Intermediate stage. (After Strasburger.) Magnified 540 times.

of the granule is made up of a number of successive layers, which have been deposited one after the other, so that the innermost layers are the oldest and the outermost the youngest. The oldest part of the granule round which all the layers have been formed is called the *hilum*. It does not necessarily lie at the centre, for sometimes the layers are deposited very unequally, so that in an old granule the hilum is in a very eccentric position. This is always the case in potato starch.

In a green plant starch is formed in two quite different ways. First it is formed in the chlorophyll granules under the influence of sunlight. It is easy to demonstrate the presence of small starch granules in the chlorophyll-corpuscles of a Wallflower leaf, after exposure to light. These starch granules are the product of carbon-assimilation—that is to say, they are formed by the chlorophyll-corpuscles in sunlight as the result, though not the direct result, of the decomposition of carbon dioxide and water, and the rearrangement of their elements.

But starch is also formed in the deep-seated tissues of the stem and the root, *i.e.* in parts which receive little or no light, and in which there is no chlorophyll. This starch cannot be the product of assimilation, for it is formed under conditions which render assimilation impossible.

What happens is this: the starch formed in the chlorophyll granules is converted into sugar,[1] and in this soluble form passes down into the stem and root. When it has reached the cells in which starch is to be deposited, the sugar is taken up by certain cyto-

[1] See, however, p. 213.

plasmic bodies, which are essentially similar to chlorophyll-corpuscles without the chlorophyll. These cytoplasmic corpuscles (called *leucoplasts*) [1] use up the sugar to re-form starch granules (see Fig. 15, *l*).

It is evident that the function of the leucoplasts is dependent on that of the chloroplasts, for unless the latter carried on the work of assimilation there would be no supplies of sugar available for the use of the leucoplasts. Starch is a very important reserve food-substance, and is very commonly found stored up in seeds, tubers, and fleshy roots, and, in fact, in organs of almost every kind. It is especially important inasmuch as it affords the material for new cell-walls, but it is used in many other ways also. Starch belongs to the great group of organic bodies called *carbohydrates*, which all consist of the three elements, carbon, hydrogen, and oxygen, the two latter elements being present in the same proportion as in water, H_2O. Sometimes we find carbohydrates stored up in the form of some kind of sugar, as in many fruits and in Beetroot. These and some other forms of reserve carbohydrates are always dissolved in the cell-sap.

γ. Oil

In many plants we find that the place of carbohydrates is taken by various kinds of oil. Oils are especially common as reserve food-substances in seeds,

[1] The word *plastid* is a general term, including *leucoplasts*, chlorophyll-granules, or *chloroplasts*, and also cytoplasmic bodies which contain other colouring matters (*chromoplasts*). The three kinds of plastids are convertible into one another; they usually arise by the division of pre-existing plastids.

e.g. Castor-oil seed, Hempseed, Linseed, etc. Oil contains the same elements (C, H, O) as carbohydrates, but in different proportions, the proportion of oxygen being very much less. The oil occurs in the form of small drops embedded in the cytoplasm.

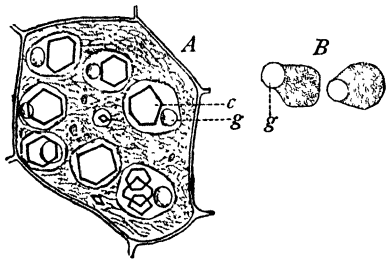


FIG. 16.—*A*, Cell from the endosperm of the Castor-oil seed, examined in water; note the large protein granules, each of which contains one or more crystalloids (*c*), also composed of protein, and *globoid* (*g*), of calcium-magnesium phosphate. *B*, Isolated granules, examined in olive-oil. (After Strasburger.) Magnified 540 times.

b. Protein Granules

These form a very important part of the contents of certain cells, especially in seeds and other organs in which food is stored up for the use of the plant. They are chemically similar to the substances of which the protoplasm is composed, but are themselves inactive, and serve simply as food. An example is shown in Fig. 16, which represents the complex protein granules of the Castor-oil seed.

c. Cell-Formation

Cells increase in number entirely by division. Every cell which exists owes its origin to the division into two or more parts of some cell which existed before it. At present we will only describe the kind of cell-formation which goes on in the vegetative parts

of plants such as the Wallflower, and indeed in all plants except the lowest. Wherever new organs are in course of development we find cell-division going on, as, for example, at all growing-points whether of stem or root. We will suppose that the cell which is about to divide has a single nucleus to start with, as is generally the case. The first obvious changes which take place are in the nucleus. The changes gone through

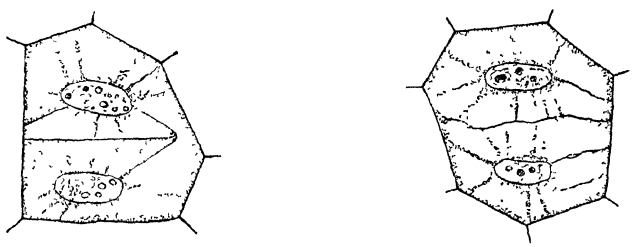


FIG. 17.—Dividing cells from the young seed of *Fritillaria*. *A*, The two daughter-nuclei have been formed, but the new cell-wall between them does not yet reach across the cell. *B*, Later stage; the new cell-wall now completely divides the mother-cell into two parts. (After Strasburger.) Magnified 240 times.

are of a very complicated character, but their ultimate effect is that the nucleus becomes divided into two exactly equal and similar parts, the *daughter-nuclei*. So precise is the accuracy of the division, that every single minute fibril of which the framework of the parent nucleus consists is split lengthways into two identical halves, one of which goes to each of the daughter-nuclei. The latter remain for a time connected by delicate threads of cytoplasm.[1] The new cell-wall is formed at right angles to these threads

[1] The details of nuclear division, a subject of the highest possible importance, must be studied in more advanced text-books.

and midway between the two daughter-nuclei. It is formed by the protoplasm itself. Generally the new cell-wall does not stretch all the way across the cell, but has to be completed at the sides later on (see Fig. 17). The nucleoli disappear during the division, and their substance appears to pass out into the cytoplasm. New nucleoli make their appearance in each of the daughter-nuclei, which soon assume the size and structure of the nucleus before division. We see, then, that the essential points in vegetative cell-formation are the division of the nucleus into two exactly similar halves, and the formation of a cell-wall between them, separating the cytoplasm of the cell into two distinct parts.

d. Continuity of the Protoplasm

We have hitherto been considering the structure of the individual cells of which a plant is built up; it has been shown, however, that in all vegetable tissues, the protoplasm of each cell is in communication with that of its neighbours by means of excessively fine cytoplasmic fibrils, which extend through the cell-wall from one cell to another. The perforations through which the connecting cytoplasmic fibrils pass are extremely minute, but are often very numerous (see Fig. 18). The importance of the discovery lies in the fact that we now know that the living matter in the plant is continuous, and not absolutely severed into isolated portions by dead cell-wall. The plant, in fact, is, as a whole, a living protoplasmic body, supported, but not interrupted, by the skeleton of cell-walls.

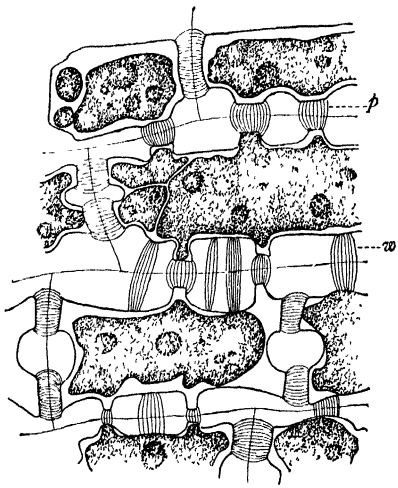


FIG. 18.— Cells from the endosperm of the seed of a Palm (*Bentinckia*), showing the fine strands of cytoplasm connecting the cells. Some (*w*) pass through the full thickness of the wall, others (*p*) through the thin places or pits. (After Gardiner.) Magnified 550.

e. Protoplasmic Movements

A good example of protoplasmic movement is afforded by the cells of the leaf of the American Water-weed (*Elodea canadensis*), a transatlantic alien, which is a great deal too common in our slow-moving water-ways. In order to see the movements of the protoplasm, a young leaf is removed from the stem and examined in water under the microscope. The movements may not begin at once ; in cold weather they are especially sluggish, but can be hurried on by gently warming the slide with the leaf upon it over hot water.

The blade of the leaf is only two cells thick, except at the midrib, where it is thicker. The cells of the midrib are long and narrow, those of the rest of the blade are shorter and broader. The movement generally begins first in the long narrow cells.

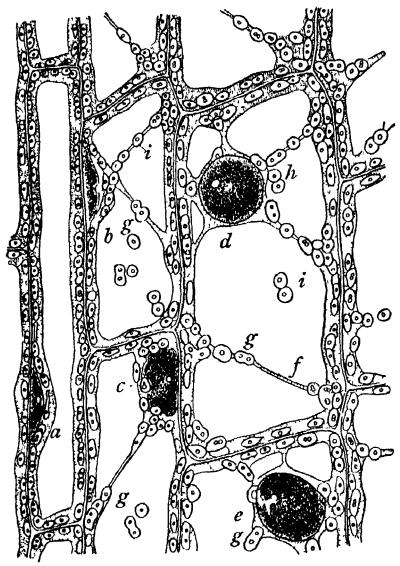


FIG. 19.—A few cells from the leaf of the American Waterweed. *a, b, c, d, e,* nuclei of the various cells; *f,* a strand of cytoplasm crossing the cell-cavity; *g, h, i,* chlorophyll granules, some of which are dividing. The small bodies inside the chlorophyll granules are starch. (After Kny.) Magnified several hundred times. The narrow cell, to the left, would show *rotation*; the broader cells, to the right, *circulation.*

Each cell has a fairly thick layer of cytoplasm (*primordial utricle*) lining its cell-wall, and in this cytoplasm numerous large chlorophyll granules are

embedded (see Fig. 19). The nucleus is very transparent, and hard to see. (It is shown dark in Fig. 19.) The cytoplasm flows in a continuous stream round and round the cell, carrying the chlorophyll granules with it. Owing to the presence of these granules, the movement is very easy to follow. If we fix our eye on one of the granules which is being swept along by the cytoplasmic stream, we shall see it travel steadily along one of the side-walls until it reaches a corner of the cell. Here there may be a momentary hesitation, for at these points the current is often choked by the accumulation of chlorophyll granules. Soon, however, the movement goes on again; the granule is carried along the short end-wall of the cell, the next corner is reached and turned, and the journey continued along the other side-wall, and so on until the circuit is complete. The revolving cytoplasm here forms one single stream, which flows round the whole cell. The current, as we have seen, follows the lateral and terminal walls of the cell. What, then, is the behaviour of that part of the cytoplasm which is in contact with the other two walls, those, namely, which form as it were the roof and floor of the cell? This cytoplasm also takes part in the general movement of rotation, and revolves in the same direction as the rest. But it has a shorter distance to cover, and the nearer we approach to the middle of the top and bottom walls, the shorter is the circuit, and consequently the slower is the speed. Now, just in the middle of each of these two walls there is a band of cytoplasm which does not move at all, but forms a

quiet eddy in the stream. This still part is called the *indifferent band*, and it is always present where rotation of the cytoplasm goes on.

But even in the other parts of the cell it is not really the whole cytoplasm which rotates. The *ectoplasm*—that is, the thin outer layer in immediate contact with the cell-wall—remains stationary, while the revolving *endoplasm* (containing the chlorophyll granules) travels over its inner surface.

This will serve to represent an important type of protoplasmic movement—that of *rotation*.

Another form of movement may often be observed in the broader cells of the lamina of the *Elodea* leaf (see Fig. 19). Here the vacuole of the cell is traversed by strands of cytoplasm, most of which are attached to the nucleus, which is here suspended in the cavity of the cell. In these cells the cytoplasm is in active movement in all directions. The strands crossing the cavity show active currents by which chlorophyll granules are often swept along. In the thicker strands there may be two opposite currents flowing simultaneously. The inner layer of the cytoplasm lining the cell-wall is also in movement, but not as in the first case all in one direction, for here there are varying streams running in different directions in different parts of the layer. Neither the arrangement nor the direction of movement of the protoplasm is constant. Sometimes a cytoplasmic strand is snapped in two, and both halves drawn back into the main mass. Sometimes a new strand is put out, which extends itself across the vacuole and joins on to the cyto-

plasm on the opposite side. Moreover, in any part of the cytoplasm the movement may stop altogether for a time, and then start again, perhaps in the opposite direction to that which it pursued at first.

Cytoplasmic movement such as this, in which numerous distinct and varying currents are flowing at the same time in the same cell, is called *circulation*. In *Elodea* circulation tends to pass over into rotation; all the cytoplasmic strands become withdrawn into the primordial utricle, which then settles down into a simple movement of revolution. In circulation as in rotation the ectoplasm remains at rest.

In one form or other it is probable that the protoplasm in every active cell is in movement, and that power of spontaneous motion is the constant characteristic of all living matter. But it is often difficult to examine a cell under sufficiently natural conditions for its protoplasmic movements to be observed. When we come to consider the simpler plants, we shall meet with several other kinds of movement executed by the protoplasm.

B. The Tissues

We have now been able to form some idea of the essential points in the structure of a living vegetable cell. Of such cells and their modifications all plants consist, if we except some of the lower plants with which we are not concerned at present. We shall find, however, that the modifications undergone by many of the cells, of which the higher plants are built up, involve very considerable changes of structure.

The different kinds of cells are not distributed uniformly all through the substance of a plant. They have a definite arrangement, and the various kinds of cells are associated together so as to form more or less sharply defined layers or strands. Such an association of similar cells is termed a *tissue*. Certain kinds of tissue, again, are generally associated together, and such a combination of tissues is called a *tissue-system*.

We are now in a position to undertake the study of the internal structure of the Wallflower. We will begin with the stem, and will make ourselves acquainted with the tissues of which it is composed.

a. Structure of the Stem

The stem of the Wallflower is traversed lengthways by a number of strands of rather tough, stringy tissue. It is possible to dissect away the soft substance in which they are embedded, and so lay bare the strands themselves. If a stem be allowed to rot, it is this stringy part which will longest resist decay. Most people will have noticed at some time or other an old rotten cabbage stalk, in which all the soft parts have perished and only a network of hard, woody, interlacing strings is left behind. These strands are the *vascular bundles*. They constitute one of the systems of tissue of which the higher plants are composed. Their great function is to serve as conducting channels through which the various food-materials pass. In most cases they are also of importance as forming a supporting skeleton for the plant.

In the Wallflower the tissue of the young stem, with the exception of the vascular bundles, is soft and succulent. A part of the soft tissue lies to the inside of the vascular bundles, and between them; the remainder is situated to the outside of the bundles. The bundles collectively, together with all the tissue that lies between and within them, form the *central cylinder*; the tissue lying to the outside of the vascular bundles is called the *cortex*. The surface of the stem is covered by a definite skin, which we can easily strip off with the aid of a pair of forceps. We find that it is a very thin, colourless membrane, which, in spite of its delicacy, is fairly tough and elastic. This skin, the *epidermis*, is only found intact on the younger parts of the stem. The older portions are covered by a much thicker and harder skin, the *bark*; all the external "protective" tissues are called by the general name of *dermal* tissue, which thus includes both epidermis and bark.

We will now examine, with the help of the microscope, a transverse section cut through the stem of the Wallflower (see Fig. 20). This shows us the cut ends of the vascular bundles, and we see that they are arranged in a ring. The space inside the ring of bundles is occupied by a large-celled tissue, the *pith* or *medulla*. A similar tissue extends between the bundles as far as the cortex which surrounds them. These bands of *interfascicular* tissue (*if* in Fig. 20) are called *medullary rays*. Vascular bundles, medullary rays, and pith collectively form the *central cylinder*. This is surrounded on the out-

side by the large-celled cortex, many cells in width (*Co*), and this again by the single layer of epidermis (*Ep*).

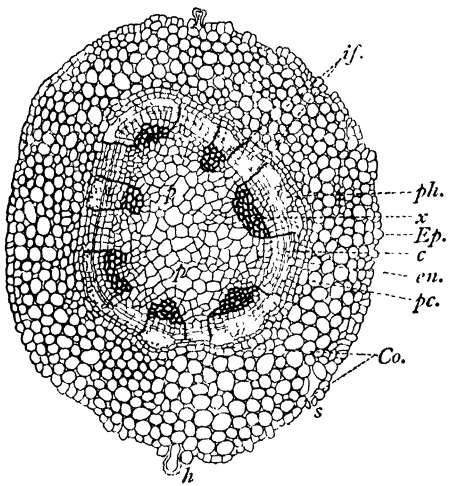


FIG. 20.—Transverse section through the second internode of the stem of a seedling Wallflower, with seven vascular bundles. *Ep*, epidermis; *h*, hair; *s*, stoma; *Co*, cortex; *en*, endodermis, or innermost layer of cortex; *pc*, pericycle, or outermost layer of cylinder; *ph*, phloëm of a vascular bundle; *x*, xylem of vascular bundle; *c*, cambium; *if*, medullary ray, or interfascicular tissue; *p*, pith. Magnified 55. (R. S.)

a. The Vascular Bundles

We will now consider the vascular bundles more in detail, and first we will determine their *course* as traced longitudinally. Each bundle runs out into a leaf. This fact is most easily proved by tracing the course of the five largest bundles, which correspond in

position to the five projecting ridges seen on the surface of the stem. It is most convenient to follow the bundle from above downwards. It enters the stem from the midrib of the leaf, runs inwards for a short distance, and then turns straight downwards, continuing its descending course in the stem through five internodes. It then reaches the leaf vertically below that from which it started, and joins on to its bundle. Besides the principal bundle, two smaller lateral bundles enter the stem from each leaf, and these behave in the same way. Hence in any transverse section of the stem we cut through about fifteen bundles, five principal strands, each representing the middle bundle of a leaf, and ten smaller strands, forming the continuation of the lateral leaf-bundles. The number is not always exact, for the smaller bundles may branch or unite together on their downward course. It is quite easy to understand the arrangement if we bear in mind that each ridge on the outside of the stem corresponds to a principal bundle, which is accompanied by its two smaller side bundles. At the nodes, *i.e.* at the insertion of each leaf, the various bundles are connected together by cross branches.

The description given applies, with slight variations in detail, to the whole stem of the Wallflower, with the exception of the first few internodes of the seedling. These have a simpler arrangement of the leaves, and consequently a smaller number of bundles. The section (Fig. 20) is taken from one of these first-formed and simpler internodes.

Vascular bundles of this kind, which are continuous

from the stem into the leaf, are called *common* bundles because they are common to both organs. That part of a common bundle which passes through the stem is called a *leaf-trace*, because its position is dependent on that of the leaf with which it is connected. We see, then, that the whole bundle-system of the stem is built up of these leaf-trace bundles, the upper ends of which run out into the leaves themselves. As the various bundles are united to one another at the nodes, it is equally easy for the food-substances which they conduct to pass out into one of the leaves or to continue their course straight up the stem, while, on the other hand, those food-substances which are formed in the leaves have ready access through the stem-bundles to all parts of the plant. In fact, the arrangement of the bundles is adapted to facilitate communication in every direction between leaf and stem. The connection with the root will be described later on (p. 78).

Where an axillary branch is given off, its leaf-trace bundles are continuous with those of the main stem.

Having described the longitudinal course of the vascular bundles, we have next to examine their internal structure. We will fix our attention on a single leaf-trace bundle, such as that which is shown in transverse section in Fig. 21.

The bundle is made up of two quite different kinds of tissue. The inner half of the bundle—that, namely, which is turned towards the centre of the stem—consists chiefly of rather large cells, the walls of which are somewhat thickened, and are hard and woody

Many of these cells are quite empty—that is to say, they have no living contents, and only contain air or water. This inner half of the bundle is the *wood* or *xylem* (*x* in Figs. 20 and 21).

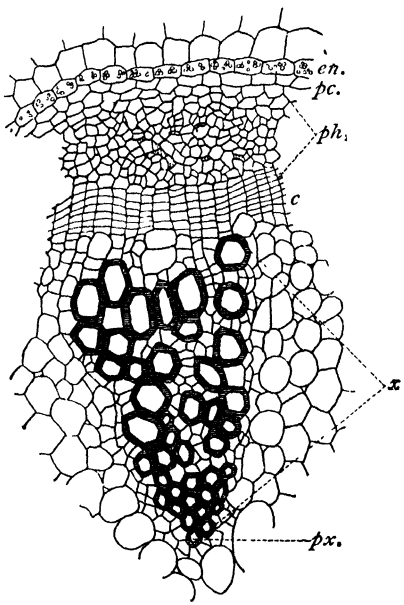


FIG. 21.—Transverse section through a vascular bundle of a young stem of Wallflower. *en*, endodermis, containing starch granules; *pc*, pericycle; *ph*, phloem; *c*, cambium; *x*, xylem or wood; *px*, protoxylem, or first-formed wood. Portions of pith, interfascicular tissue, and cortex are also shown. Magnified about 210. (R. S.)

The outer part of the bundle, lying towards the cortex, consists of much smaller cells, with thin walls of pure cellulose, and with abundant protoplasmic

contents. This part of the bundle is called the *bast* or *phloëm* (*ph* in Figs. 20 and 21).

Between xylem and phloëm is a band of very regular cells, which appear oblong in transverse section, and have very thin walls, showing that active division is going on (see Fig. 21, *c*). This layer is the *cambium*, which in plants of the Class to which the

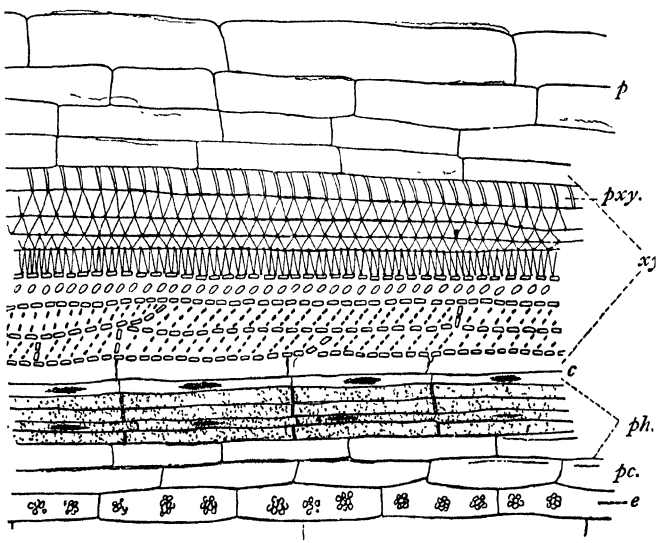


FIG. 22.—Radial longitudinal section passing through a vascular bundle from a young stem of Wallflower. *e*, endodermis, containing starch; *pc*, pericycle; *ph*, phloëm; *c*, cambium; *xy*, xylem; *pxy*, protoxylem; *p*, pith. Somewhat diagrammatic. Magnified 220. (R. S.)

Wallflower belongs is constantly undergoing cell-division, and adding new cells to the wood internally, and to the bast externally (see pp. 60 and 90).

The wood in the Wallflower consists of three kinds of elements, which are best studied in longitudinal section (see Fig. 22).

The Wood or Xylem

1. The Vessels

These are long, continuous tubes, which extend through the plant for considerable distances without any interruption. When mature, they appear empty, containing no protoplasm, but only water and air. The vessels have very peculiar markings on their walls, which are due to their being unequally thickened, some parts of the wall growing much in thickness, while other parts remain quite thin. In the vessels nearest the pith the thickening generally takes the form of a spiral thread, which winds along the inside of the wall. The parts of the wall between the coils of the spiral are quite thin. The structure of one of these *spiral vessels* is exactly like that of an indiarubber hose with a stiff spiral wire coiled inside it to prevent its collapsing. In the innermost vessels the spiral is always loosely coiled. This is because the innermost vessels are the first to be formed, and their walls become thickened before the tissues have stopped growing in length, so that as growth goes on the spiral gets drawn out.

Sometimes, instead of the continuous spiral thread, we find isolated transverse rings round the vessel, which is then called *annular*. This form also admits

of subsequent growth in length, for as the vessel becomes longer the rings become pulled farther apart. This form is not so very common in the Wallflower. These innermost vessels constitute the *protoxylem*, so called because this part of the wood is formed first, and is therefore the oldest (see Fig. 22, *pxy*).

The vessels a little farther towards the outside are still spirally thickened, but here the coils of the spiral are closer together, for the thickening has been developed a little later, and so has not got so much pulled out by subsequent growth.

Next we come to vessels in which the thickening on the walls forms a network (*reticulated vessels*), the meshes of which are occupied by a thin membrane. This form is not capable of longitudinal extension, and is only developed after growth of the stem in length is complete.

Lastly, in the outer and later-formed parts of the xylem, we find vessels in which the wall generally is thickened, but a number of little oval spaces are left thin. These vessels are said to be *pitted*, the thin parts of the wall being the pits. The pits serve for the passage of liquids from one vessel to another; the various kinds of thickening have the object of stiffening the vessel and enabling it to resist pressure.

We have seen that the vessels are open, continuous tubes. They are therefore quite different from ordinary cells such as we described above. A vessel is not a cell, but it is formed from a number of cells

Each vessel consisted at first of a whole row of superposed cells, each with its own cytoplasm and nucleus. Then the cross walls separating these cells from one another were dissolved away, and so the whole row came to form one open passage. The cross walls, however, do not disappear entirely. A ring is left at the edge, and in the Wallflower we can easily see these rings, even in the mature vessels, marking the limits between the original cells which have fused to form a vessel (see Fig. 36, p. 94). These rings are found in all vessels, and must not be confused with the rings of thickening, which are found in the annular vessels of the protoxylem only.

We have already seen that the cell-wall is formed by the protoplasm. Where, as in vessels, certain parts of the cell-wall are specially thickened, these thickening masses also are deposited by the protoplasm, which at last becomes almost entirely used up in the process. What little protoplasm remains is absorbed by the neighbouring cells, and the vessel is left quite empty. Thus the vessels when fully formed are *dead* structures; they contain no living matter, and are incapable of further growth. They serve simply as open channels through which the sap can pass.

2. The Fibrous Cells

The wood of the Wallflower also contains fibrous cells, which are scattered about among the vessels, and are more common in the later-formed parts of the wood. They are very long, thick-walled cells, with sharply pointed ends. The wall is thickened almost

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all over, but there are a few small narrow pits where the wall is left thin. These cells, unlike the vessels, keep their living contents, and do not fuse with one another. The chief function of the fibrous cells is a mechanical one; they serve to give rigidity to the stem. At the same time their protoplasm retains its activity, and consequently these cells are able to form and store up starch for future use. Tissue composed of cells of this shape, with long pointed ends overlapping one another, is called *prosenchyma*, and is commonly found where mechanical strength is required (see Fig. 36, p. 94).

3. The Xylem-Parenchyma

Besides the vessels and fibrous cells, the xylem also contains cells with square ends. They are of considerable length, though very much shorter than the fibrous cells, and have rather thick walls with small pits. They always contain protoplasm and a nucleus, and often starch granules as well, and form the chief tissue in the wood in which starch is stored up. They do not undergo fusion. These square-ended cells constitute the woody or xylem parenchyma, the word *parenchyma* being used for any cellular tissue with cells of a rounded, square, or oblong form. Cells of this kind are always found in contact with the vessels (see Fig. 36).

The woody character of the cell-walls of the xylem is due to the presence of a substance called *lignin*, a chemical modification of cellulose, which greatly alters its properties. Lignified cell-walls are much harder and stiffer than those of pure cellulose. Such walls are characteristic of the xylem, which is often a supporting as well as a conducting tissue, and then forms part of the skeleton of the plant. But we may find cells with thick, lignified walls outside the vascular bundle

altogether, or in its phloëm portion, though this is not the case in the Wallflower. The xylem, therefore, does not of necessity form the whole skeleton of the plant, and in some cases is a conducting tissue only.

In the vessels of the xylem the hard, thick, lignified, stiffening bands have a special function, for the cavity of a vessel is often almost a vacuum, only containing air at a very low pressure, and a very small quantity of water. Vessels in this state would very readily yield to the pressure of the surrounding tissues, and so collapse, if their walls were not specially strengthened.

The Bast or Phloëm

In the Wallflower the bast consists entirely of cells with soft walls of pure cellulose. The most important cells are of three kinds (see Fig. 23).

1. The Sieve-Tubes or Bast-Vessels

These are made up of long cells placed end to end. Their great peculiarity is that their end-walls are perforated—that is, bored through in a number of fine holes, like a sieve. From this fact they obtain their name. They are called vessels because the cells of which they are built up are in open communication with one another, but while in many wood-vessels the cross walls are almost entirely absorbed, in all bast-vessels they are only perforated. The sieve-tubes retain their cytoplasm, and also contain a slimy substance which is rich in nitrogenous compounds; sometimes starch grains are also present. The sieve-tubes when old may have no nuclei. Each of their constituent cells has a nucleus to begin with, but later it may disappear.

Possibly the nucleus persists as long as the sieve-tube remains functional. Where sieve-tubes are in contact with each other side by side, their lateral walls are also perforated, not all over, but in certain parts. Through the perforations, whether of the transverse or of the longitudinal walls, the contents of the sieve-tubes are continuous. We must remember that this perforation of the cell-walls and open communication between the cytoplasm of neighbouring cells is not peculiar to sieve-tubes. We have already learnt that living cells generally have their protoplasm continuous through minute perforations in their walls. The perforations in the sieve-tubes, however, are often much larger than those of ordinary cells, and continuity of the protoplasm was recognised in them long before it was even suspected to exist between other living cells. That part of the cell-wall of the sieve-tube which is perforated is called the *sieve-plate*. The sieve-plate and its pores are coated with a substance (distinct from cellulose) called *callus*, which may accumulate to such an extent as partially to close the plate (Fig. 23, *C*).

2. The Companion-Cells

The sieve-tubes are accompanied by narrow, longish cells, each of which is densely filled with cytoplasm, and contains a large nucleus, which is permanently retained. These cells are called the companion-cells. In a transverse section the companion-cells look as if they had been cut off from the corners of the sieve-tubes, and that is how they really originate, for sieve-tube and companion-cell are formed by the

division of the same mother-cell (see Fig. 23, *A*, *B*, and *C*, *z*). The companion-cells are in protoplasmic communication with the sieve-tubes.

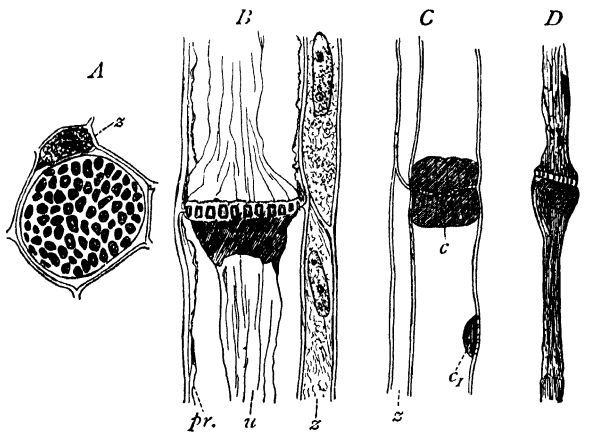


FIG. 23.—Sieve-tubes and companion-cells from the phloëm of the Pumpkin (*Cucurbita*). *A*, Transverse section, showing sieve-plate and companion-cell, *z*. *B*, Longitudinal section, showing a sieve-plate in sectional view: *pr*, primordial utricle of sieve-tube; *u*, its contracted contents; *z*, companion-cells. *C*, Longitudinal section, showing sieve-plates covered by callus *c* and c_1. *D*, Contents of sieve-tube after the cell-wall has been dissolved away with sulphuric acid. (After Strasburger.) Magnified about 400.

3. The Phloëm-Parenchyma

The rest of the phloëm is made up of rather large parenchymatous cells, which have the typical structure of living cells, each containing a layer of cytoplasm lining the wall and a single nucleus. This tissue undergoes no special modification, and is called simply *phloëm parenchyma*.

The cells at the extreme outer edge of the phloëm are the first to be developed, and are therefore called the *protophloëm.* Unfortunately, the phloëm of the Wallflower is not well adapted for showing the minute structure, as all the cells are very small in this part. It has therefore been necessary to introduce Fig. 23, taken from another plant (the Pumpkin). The phloëm, like the xylem, is partly a conducting tissue ; its special function may be to conduct nitrogenous food-substances from the leaves to the parts where growth is going on, namely, the various growing points and the cambium. It is probable that a certain amount of digestion goes on in the sieve-tubes, and that the companion-cells secrete the enzymes [1] necessary for this process.

Between xylem and phloëm there are some layers of cells which do not as yet show the characters of either tissue. On the inner side these layers pass over gradually into xylem, and on the outer side into phloëm. The layer in the middle is itself constantly dividing, and thus contributing new elements to wood and bast respectively. The thinnest walls indicate the most recent divisions (see Fig. 21). The divisions take place chiefly in the tangential direction—that is to say, in the direction of the line separating xylem from phloëm, which is parallel to a line tangential to the surface of the stem at a point opposite the bundle. As already mentioned, it is characteristic of the class to which the Wallflower belongs to have this actively dividing layer of *cambium* between the xylem and phloëm. Vascular bundles which have a cambium are known as *open* bundles, because there is no definite limit to their growth in thickness, the formation of

[1] Enzymes are substances of complex composition, in the presence of which certain chemical changes are rapidly effected, changes which under other conditions proceed slowly and perhaps so slowly as to be negligible. For instance, starch is rapidly transformed into sugar in the presence of the enzyme *diastase.* Individual cells of animals and plants may contain many kinds of enzymes.

new xylem and phloëm from the permanently active cambium going on as long as the plant lives. We shall, however, understand the nature of the cambium better after we have considered the development of tissues in the growing points.

β. Other Tissues of the Central Cylinder

The central cylinder consists of the vascular bundles and of parenchyma, which is called *conjunctive* tissue because it unites the bundles together. That part of the conjunctive tissue which lies inside the ring of bundles, and is called the pith, is of very simple structure. It is made up of large, rather elongated, square-ended cells (Fig. 22, *p*), which retain their living contents, and usually form starch granules. The *interfascicular* tissue, constituting the medullary rays, is similar to the pith, but its cells are smaller. It is important, because its cells divide up to form the *interfascicular cambium*, which unites the cambial layers of the separate bundles into a continuous ring of actively multiplying cells (see Figs. 20 and 21). Owing to the presence of this layer of cambium, the stem is able constantly to form new tissues, and thus to grow indefinitely in thickness (see below, p. 90).

Surrounding the whole ring of vascular bundles on the outside is a layer of thin-walled cells, the *pericycle* (*pc* in Figs. 20, 21, and 22). This layer forms the outer limit of the central cylinder. Beyond this we come to the cortex.

Those cells of the conjunctive tissue which border on the vascular bundles are generally rich in grape-sugar, dissolved in their cell-sap. It is chiefly through

these cells that the carbohydrates pass on their way from the leaves to other parts.

γ. *The Cortex*

Adjoining the pericycle on the outside is a single layer of cells, with slightly thickened walls, and with numerous starch granules in their contents. This layer is the *endodermis* (*en* in Figs. 20 and 21, *e* in Fig. 22), and forms the inner limit of the cortex. The rest of the cortex consists of ordinary parenchyma, like that of the pith. Its outer layers, however, have rather thick walls, though they consist of pure unlignified cellulose. The outer cells contain chlorophyll-granules, and can therefore take some part in carbon-assimilation, though this function belongs chiefly to the leaves. The thick-walled layers are of some mechanical importance in helping to give greater stiffness to the stem.

Parenchymatous cells generally, whether belonging to the central cylinder or to the cortex, do not as a rule fit closely together, but separate slightly from one another at their corners so as to leave little spaces between them. These *intercellular* spaces, as they are called, contain air and aqueous vapour, but not water.

δ. *The Epidermis*

The epidermis of the stem is one layer in thickness. The epidermal cells are of three different kinds; the ordinary cells are elongated, with square or sometimes pointed ends, and fit closely together without any intercellular spaces. These cells each contain cytoplasm and a nucleus, but no chlorophyll-

granules. The outer layer of the superficial cell-wall of the epidermis forms the cuticle, and does not consist like the other walls of cellulose, but of a substance (*cutin*) resembling cork, which is extremely impervious to water and water vapour, and which is chemically a remarkably stable body, resisting the action even of strong sulphuric acid, and of other substances which easily dissolve the cellulose. The inner and lateral walls of the epidermal cells consist simply of cellulose, and the same is the case with the innermost layer of the superficial wall.

The epidermis of the Wallflower bears very large and characteristic *hairs*. Each hair is a single cell. It has the form of a spindle, and is attached at the middle by a short stalk, which is inserted between the ordinary epidermal cells (see Figs. 26, 27, and 43, which show similar hairs on the leaf). These hairs are always so placed that the spindle lies close to the surface of the epidermis, and parallel to the axis of the stem. They have an external cuticle, like other epidermal cells. Their surface is rough, with projecting knobs, which contain calcium carbonate (chalk). Experiments have shown that these rough and sharp hairs are of great importance to the plant, as a protection against the attacks of slugs and snails.

It has already been mentioned that the ordinary epidermal cells have no intercellular spaces between them. There are, however, intercellular spaces in the epidermis, but they only occur at definite points, between specially modified cells. Such a space, with the cells which enclose it, is called a *stoma*.

Each stoma consists of a pair of cells, much smaller than those of the epidermis generally, and of quite a different form (see Fig. 20, *s*, also Figs. 26 and 27, *s*, from leaf). These two cells are called the *guard-cells*. Each guard-cell is sausage-shaped and curved, the ends of the cells being firmly joined together, while in the middle they are separated a little, leaving a narrow pore or chink between them, which communicates with the intercellular spaces of the ground tissue. The guard-cells of the stomata differ from other epidermal cells in containing chlorophyll-corpuscles and starch granules. We will defer the more detailed consideration of the structure of the stomata until we come to the leaf, where their more important functions are discharged.

b. Structure of the Leaf

We have already learnt so much of the structure of the leaf as can be made out with the help of a lens only (see Fig. 7). The leaf is built up of the same tissues as we have found in the stem, but with many differences in arrangement and in the details of structure.

The vascular bundles of the leaf are the direct continuation of those in the stem. We have already traced the general course of the veins of the leaf, and this is identical with the course of the vascular bundles, each vein corresponding to a bundle. In the larger veins, however, such as the midrib, the bundles are accompanied by a massive, enveloping zone of parenchyma, differing from that of the rest of the leaf in containing little chlorophyll and plenty of starch. The principal bundle traverses the midrib from

end to end, tapering towards the apex of the leaf, and giving off branches on either side. All these branches ramify repeatedly, but always in the same plane, the successive offshoots becoming finer and finer, until we come to the extremely slender ultimate branchlets, which end blindly within the meshes formed by the larger bundles (see Fig. 24).

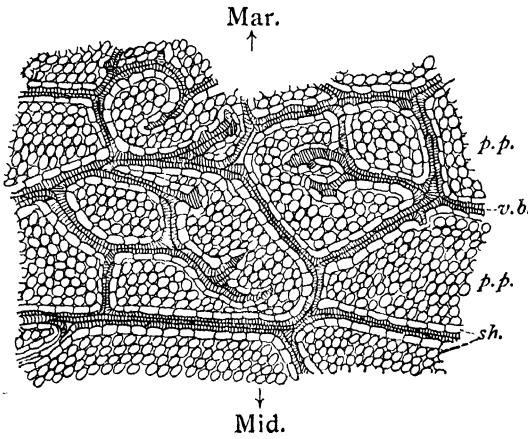


FIG. 24.—Part of a section, parallel to the surface, of a leaf of the Wallflower, passing through the palisade parenchyma, and showing the xylem of the bundles as seen from above. Observe the *endings* of the bundles within the meshes. *p.p*, palisade parenchyma; *v b*, vascular bundle; *sh*, bundle-sheath. The arrows point towards the margin and the midrib of the leaf respectively. Magnified 50. (R. S.)

The two lateral bundles also branch immediately on entering the leaf, and form the bundle-system of the basal part of the lamina.

The larger vascular bundles of the leaf agree in

structure with those of a young stem, but the two parts of the bundle are so placed that the xylem is directed upwards, and the phloëm downwards. This is a constant rule for vascular bundles in flat leaves, and holds good both for the main bundles and their branches. We know that in the stem the xylem faces inwards and the phloëm outwards, and as the bundle passes into the leaf without any twisting, the xylem necessarily comes to lie towards the upper, and the phloëm towards the lower surface of the leaf.

The loosely coiled spiral vessels of the protoxylem are found at the extreme upper edge of the wood, while the protophloëm lies at the extreme lower edge of the bast. The development of the parts of the bundle follows precisely the same order as in the stem. In the leaf, however, the bundles are *closed*. The life of the leaf being limited, there is no need for a permanently active cambium.

In the finer bundles of the leaf the structure is greatly simplified, the xylem consisting exclusively of spirally thickened elements. In the ultimate branches these elements are of the kind called *tracheids*; they resemble vessels in all respects except that the cells of which they are composed do not fuse with one another, so that they do not form continuous tubes. If we trace the finest bundles to their termination, we find that the phloëm comes to an end before the xylem, so that the extreme end of the bundle consists of spiral tracheids only. All the bundles, including their finest branches, are enclosed in

sheaths of closely-fitting parenchymatous cells (see Fig. 24).

We must now say something as to the tissue which surrounds the vascular bundles in the larger veins of the leaf, especially in the midrib (see Fig. 25). The parenchymatous tissue of the midrib contains but little chlorophyll, and closely resembles the cortical tissue of the stem. The cells towards the upper and lower surfaces of the midrib are rather thicker-walled than the rest. The other main veins of the leaf show a somewhat similar structure on a much smaller scale. Together with the midrib they form a mechanical supporting system for the leaf, constituting a stiff framework, between the ribs of which the delicate tissue of the lamina is extended, and thus kept in position. The larger bundles also have a little parenchyma within their sheath.

Now we will consider the structure of the chlorophyll-containing tissue (*mesophyll*), of which the thin, deep-green lamina chiefly consists.

On examining a transverse section (see Figs. 25 and 26) we see at once that the parts of this tissue towards the upper and lower surface respectively have a different structure. The upper part of the mesophyll is made up of three or more layers of closely-packed cells, which are elongated in the direction at right angles to the surface of the leaf. These cells contain an immense number of chlorophyll-corpuscles embedded in their protoplasm, and chiefly ranged on the side-walls of the cells (see Fig. 26). From the appearance of its upright and regularly arranged cells this

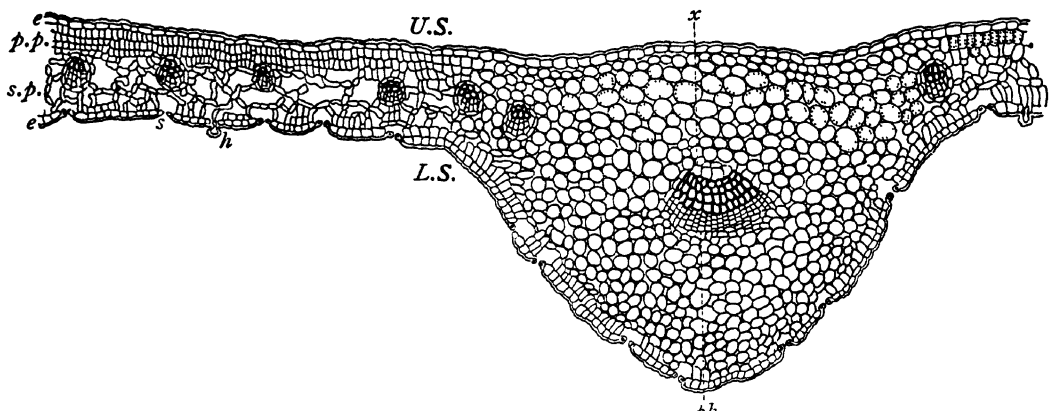


FIG. 25.—Transverse section through part of the leaf of the Wallflower, passing through the midrib. *e*, epidermis; *h*, hair; *s*, stoma; *p.p*, palisade parenchyma; *s.p*, spongy parenchyma; *x*, xylem of largest bundle; *ph*, phloem; *U.S.*, upper surface; *L.S.*, lower surface, of leaf. Magnified about 35. (R. S.)

tissue is called the *palisade parenchyma.* Its cells are cylindrical in form, and have narrow intercellular spaces between them.

The lower half of the mesophyll, on the other hand,

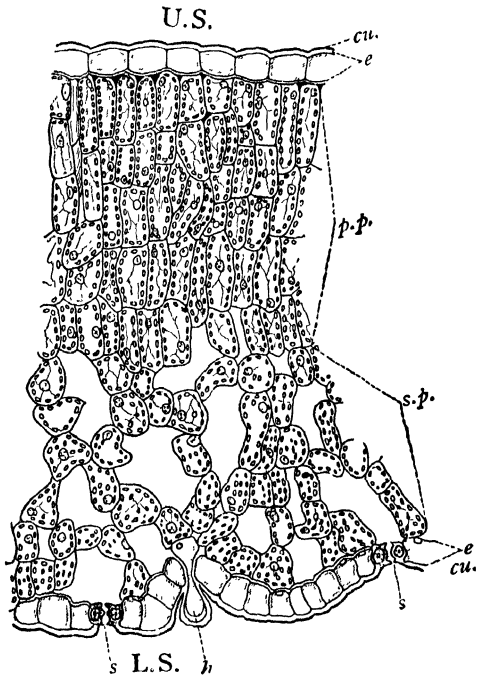


FIG. 26.—Part of a transverse section of a leaf of the Wallflower. *e*, epidermis; *cu*, cuticle; *p.p*, palisade parenchyma; *s.p*, spongy parenchyma; *s*, stoma; *h*, hair; *U.S.*, upper, *L.S.*, lower, surface of leaf. Magnified 165. (R. S.)

consists of very loosely arranged irregular cells, with very large air spaces between them. These cells, like those of the palisade parenchyma, contain chlorophyll-

corpuscles, but they are less numerous here, and are distributed uniformly in the cytoplasm lining the cell-walls. This tissue is called the *spongy parenchyma.* The lower ends of the palisade cells never end blindly in an intercellular space, but always join on to cells of the spongy parenchyma.

The finer vascular bundles pass through the upper part of the spongy tissue in such a position that their xylem almost reaches the lower ends of the palisade cells.

The differentiation of the mesophyll into palisade and spongy tissue is characteristic of those flat leaves which are horizontal, and which therefore have an upper and a lower surface. Both tissues take part in carbon-assimilation, the palisade-parenchyma being specially adapted to the intense light which falls on the upper surface of the leaf. The spongy parenchyma is actively concerned in the transpiration of water vapour (see Chap. III., p. 220).

The *epidermis* of the upper surface of the leaf consists entirely of closely-packed cells, without intercellular spaces. It bears a few long, spindle-shaped hairs, like those of the stem. There are no *stomata* on this upper surface.

The epidermis of the lower surface has more numerous hairs, and possesses an immense number of stomata (see Fig. 27). The general structure of a stoma has already been described. Each stoma opens into a large intercellular space in the spongy tissue immediately within it. This space is called the *air-chamber* (see Fig. 26). The air-chambers, again, are in communication with all the intercellular spaces of the leaf, and through them, with those of the whole plant. The stomata, then, are the pores by

which the intercellular passages of the whole plant, containing air and water vapour, open into the external atmosphere.

A section across a stoma shows the two guard-cells with the pore between them (Fig. 26). The transverse section of each guard-cell is roughly a square; the walls are very thick, especially at the two corners

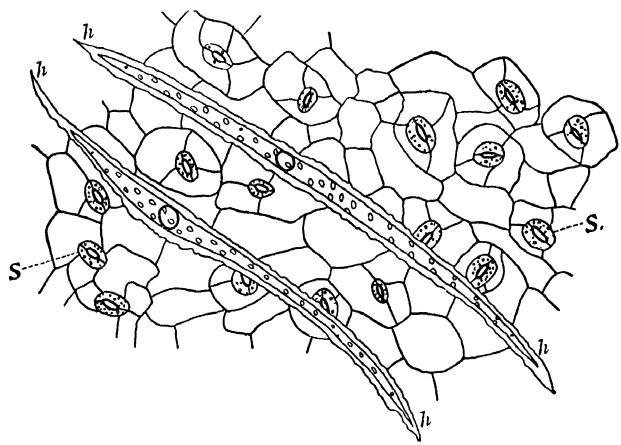


FIG. 27.—Portion of epidermis from the under side of a Wallflower leaf, in surface view. *h*, *h*, hairs; *S*, *S*, stomata. Magnified about 210. (R. S.)

towards the pore, which are provided with projecting ridges. We have already learnt that the guard-cells contain chlorophyll-corpuscles and starch granules, and thus differ from the ordinary epidermal cells.

The stomata have the power of opening and closing. As a general rule, they open under the influence of light and warmth, and close when it is dark or cold.

The pore opens when the guard-cells become more curved, so that the space between them is widened. It closes when they straighten, so that their sides are brought into contact. We shall see later on how this opening and closing of the stomata works in with the mode of action of the leaf as a whole (see p. 221).

c. Structure of the Root

We will now examine the structure of the main root or *tap-root*, which forms the direct downward continuation of the stem. It does not differ essentially from its branches, but has the advantage of being rather larger, and more convenient for investigation.

In order to find the primary structure of the root unaltered, we must take a very young one; for in the Wallflower, and most members of its Class, the cambium begins its activity early, and soon brings about a complete change in the distribution of the tissues.

We will start as before with the vascular system, which at first sight appears very different from that of the stem. The middle of the root is traversed by a slender cylindrical strand of vascular tissue, which runs in a straight course from base to apex, and is directly continuous with the bundle-system of the stem. In a root which has reached the stage shown in transverse section in Fig. 28, the xylem forms a plate of tissue passing through the centre of the vascular cylinder; the phloëm is grouped in two distinct bundles, one on each side of the xylem-plate. If we had examined a still younger root, we should have found that only the cells at the two ends of the

xylem-plate were mature and lignified, the middle part of the plate consisting of thin-walled cells still in course of development. In other words, the

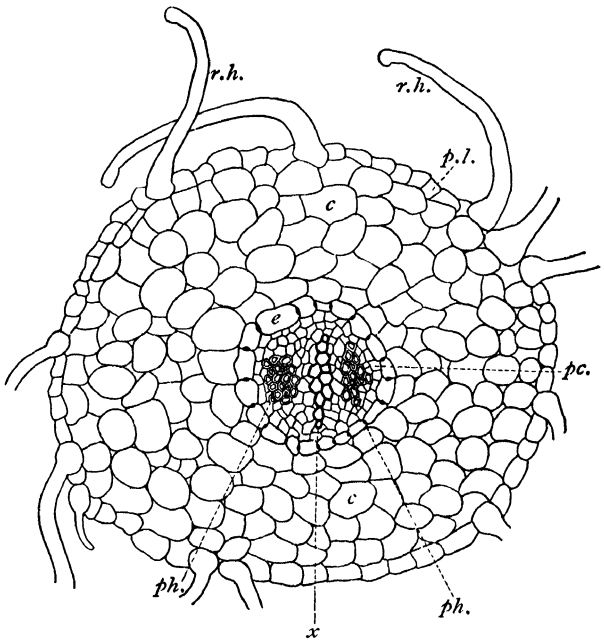


FIG. 28.—Transverse section of a very young root of the Wallflower. *r.h*, root-hairs; *p.l*, piliferous layer; *c*, cortex; *e*, endodermis; *pc*, pericycle; *x*, xylem-plate; the protoxylem is at its two ends; *ph*, *ph*, the two phloem groups. Magnified 110. (R. S.)

protoxylem, or oldest wood, of the root is formed at the outside, and development advances from without inwards, just in the reverse order to that which is followed in the formation of xylem in the stem

Consequently we should have to look for the first-formed spiral vessels at the extreme ends, as seen in a transverse section, of the xylem-plate of the root. The phloëm develops from without inwards, just as in the stem, so we see that, in the root, wood and bast are both formed in the same direction, and not in opposite directions, as in the stem. We find that in this root there is no pith, for the wood extends quite to the centre. This is characteristic of very many roots, though not of all. There are a few parenchymatous cells between xylem and phloëm; these cells form the conjunctive tissue of the central cylinder.

A root with the structure just described is called *diarch*, because there are, to begin with, two groups of xylem and two of phloëm, the two xylem groups soon uniting in the middle to form the continuous plate. When there are three groups of each, the root is called *triarch*; when four, *tetrarch*; and so on.

We see that the arrangement of the xylem and phloëm is quite different in the root and in the stem. While in the latter the xylem always lies just inside the phloëm, the two together forming a collateral bundle, in the former the bundles of xylem and phloëm are distinct, and alternate with each other all round the vascular cylinder (cf. Fig. 64, p. 165).

The arrangement in the root may be called *radial*, because the xylem and phloëm groups are placed on alternate radii of the central cylinder, which, as seen in transverse section, is almost circular. The chief points, then, in which the vascular system of the root differs from that of the stem are—

(1) The alternating arrangement of the xylem and phloëm groups.

(2) The centripetal development of the xylem.

(3) The greater concentration of the bundles, and consequent smaller diameter of the central cylinder, which contains but little parenchyma between the bundles, and often has no pith.

The vascular cylinder is surrounded by a layer of thin-walled cells, the *pericycle*, which here, as in the stem, forms the outermost layer of the cylinder. In the root this layer is of special importance, for from it all the branches of the root arise.

The *pericycle*, again, is surrounded by another layer, the *endodermis*, which here has the peculiarity that its cell-walls, in so far as they border on other endodermal cells, are cuticularised. This is not the case with the inner and outer walls, which abut on the pericycle and cortex respectively. We can recognise the endodermis in the root in transverse sections by the dark appearance of its cuticularised radial walls (see Fig. 28, *e*); we know that cuticularised walls resist the passage of water much more than cellulose walls do, so the effect of this arrangement is that water has free passage through the endodermis from the cortex into the vascular cylinder, but cannot turn aside to pass from one endodermal cell into another. The cuticularised walls of the endodermal cells fit closely together, so that the intercellular spaces of the cortex are completely shut off from those of the cylinder. This structure of the endodermis is sometimes found in the stem also, but not so constantly as in roots. The endodermis is

really the innermost layer of the cortex. The rest of the cortical tissue consists of living parenchymatous cells, with thin cellulose walls. They do not, of course, contain any chlorophyll, because the roots in the earth receive no light, without which chlorophyll cannot be formed, though the plastids may be present.

The outermost layer of the young root, corresponding in position to the epidermis of the stem, consists of thin-walled living cells, many of which grow out into long hairs (see Fig. 28). These root-hairs are very important organs; they take up all the food which the plant obtains from the soil. Each root-hair is a single cell, with cytoplasm and a nucleus, and a thin cell-wall. The delicacy of the outer cell-walls, and the absence or slight development of cuticle, are points in which the external layer of the root differs from the epidermis of the shoot. The meaning of these differences is, that the epidermis of the stem is a *protective* layer, which among other duties has to hinder the passage of water out of the plant, while the external tissue of the root is *absorptive* (so long, that is, as the root is quite young), and has to admit into the plant water and various food-substances which are dissolved in it. Partly because of this great difference in function, and partly on account of some differences in the development, it is better not to speak of the external layer of roots as an epidermis, but to call it the *piliferous* layer, *i.e.* the layer which produces the root-hairs.

These root-hairs grow between the small particles of soil, and attach their ends to them quite firmly, so

that it is impossible to pull up a plant out of the ground without lifting with it innumerable fragments of soil, which remain sticking to the hairs on the young roots so firmly that they cannot be washed off. This adhesion to the soil is due to the conversion of the outer layer of cell-wall into mucilage. The student must be very careful never to confuse the

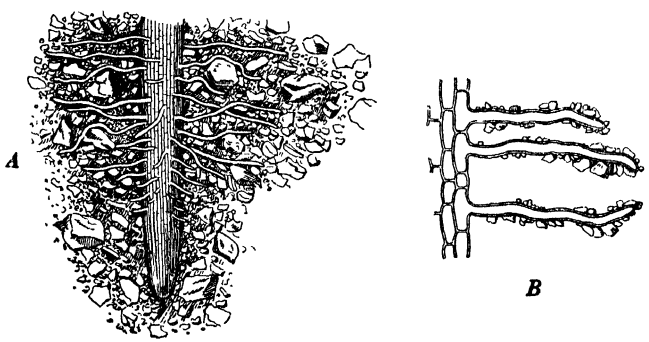


FIG. 29.—*A*, Young root, with root-hairs penetrating the soil. Magnified about 7 times. *B*, Root-hairs more highly magnified, showing their close adhesion to the particles of soil. (After Kerner.)

root-hairs with the finer branches or fibres of the root itself. The latter may appear thin to the naked eye, but they are very thick in comparison with the hairs, and always have the same structure as the main root on a smaller scale, while, as we have seen, the root-hair is a single long cell (see Fig. 29).

The root bears no leaves: its only appendages are—(1) the rootlets, which repeat in essentials the structure of the root which bears them; and (2) the hairs.

The growing point of the shoot is, as we know

protected by the leaves of the terminal bud, which close in over it. The growing-point of the root requires protection even more, for it has to make its way between the hard particles of the soil, and hence a special organ is present which performs this sheltering function. This organ is the *root-cap*, a sheath of tissue shaped rather like a thimble, which envelops the delicate growing apex. As the root elongates, the cap is pushed before it, and has to bear the brunt of the friction with the soil (see Figs. 33 and 34, *c*). The outer layers of the root-cap become gradually converted into mucilage, which serves both to diminish the friction and to keep the apex moist, and as this happens, the cap is renewed from within by the growing point itself, which thus has to provide new tissue for the cap in front of it as well as for the body of the root behind (see Fig. 33, *c*).

The presence of the cap is another very constant character by which roots are distinguished from stems.

d. Transition from Stem to Root

It has already been said that the tissues of the root are continuous with those of the stem. We will now see how the one organ passes into the other. In order to understand this, it will be necessary to study a fairly young seedling, before there has been much growth in thickness.

The first two leaves which the Wallflower seedling forms are placed opposite to one another, as is almost always the case in the class of which it is a member. These two first leaves are called the *seed-leaves* or *cotyledons*, and differ considerably from the other leaves of the plant. For example, they are nearly round in

shape, and have distinct leaf-stalks, their venation is also different from that of ordinary leaves, and the hairs mostly have three or more arms. The part of the stem which comes below the cotyledons, *i.e.* between them and the tap-root is called the *hypocotyledonary stem* or *hypocotyl* (*hyp* in Fig. 30). It is in this region that the transition between stem and root structure takes place. From each cotyledon we can trace two vascular bundles into the hypocotyl. As soon as they enter it they are joined by the bundles of the next leaves above; but with these we need not concern ourselves, for only the bundles of the cotyledons extend down into the root. The hypocotyl, therefore, contains four vascular bundles only, two on each side. Their position is different from that of the ordinary vascular bundles of the stem. In each pair the two protoxylem groups are united, and not directed inwards, but are turned towards the periphery; this is the case even in the cotyledons themselves, before the bundles have entered the hypocotyl. The rest of the xylem forms two distinct groups (*metaxylem*[1]) in each pair. The phloëm groups are not placed directly opposite the xylem, but lie rather farther to the right and

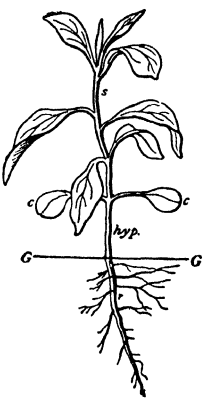


FIG. 30.—Wallflower seedling. *s*, stem; *c*, *c*, cotyledons, or first leaves; *hyp*, hypocotyledonary stem; *G*—*G*, level of ground; *r*, root. One-half natural size. (R.S.)

[1] The word *metaxylem* is applied to that part of the primary wood which is formed after the protoxylem.

left, so that in each pair of bundles the two groups of phloëm are farther apart from each other than are those of the xylem. Now, the farther we trace the vascular bundles downwards, the nearer to each other do we find the xylem groups of each pair, and as they approach each other their protoxylem keeps its peripheral position, on the right and left (see Fig. 31, *px*). Lower down still we find in place of each pair of xylem groups a single one, with its protoxylem still directed straight outwards. The two bundles of each pair are at no time so separate as to possess distinct protoxylem-groups; there is a single, central, and common protoxylem throughout, the position of which, with reference to the rest of the xylem and the phloëm, varies according to the level. Ultimately the whole of the xylem on each side becomes united. From this point onwards, the hypocotyl contains two groups of xylem only, and these groups now converge, and ultimately unite to form the diarch xylem-plate of the root itself. We see, then, that this

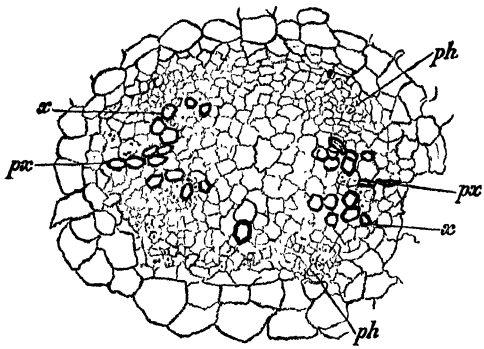


FIG. 31.—Part of transverse section of hypocotyl of Wallflower, showing cylinder. *px, px*, protoxylem groups of the four bundles from the cotyledons; *x, x*, metaxylem; *ph, ph*, phloem groups of right-hand pair. From the middle of the transitional region between stem and root. Magnified about 200. From a drawing by Dr. Ethel N. Miles Thomas, F.L.S.

xylem-plate forms the downward prolongation of the two pairs of xylem strands from the cotyledons. Consequently the xylem-plate lies in the vertical plane which passes through the insertion of the two cotyledons.

In the Wallflower and many other Dicotyledons, the outwardly directed protoxylem is not only a character of the root, but is common also to the hypocotyl and the cotyledons.

In the meantime, we find a corresponding change in the position of the phloëm strands, but in the reverse direction. The two phloëm strands of each pair of vascular bundles diverge more and more from each other, until the right-hand group of one pair meets the left-hand group of the opposite pair, and *vice versâ* (see Fig. 31, *ph*). Tracing them still farther down, we find that these two groups become one, so that at last there are only two groups of phloëm altogether, one on each side of the xylem plate. Each phloëm strand of the root, then, is continuous with two phloëm strands of the hypocotyl, one belonging to each cotyledon, and thus we see that in spite of the great difference in the arrangement of the xylem and phloëm strands, the vascular system of the main root is the direct downward continuation of that of the stem, the hypocotyl forming the connection between the two; the parenchyma of the central cylinder undergoes a great reduction in the transitional region, the pith gradually disappearing as the bundles converge. The pericycle forms the external layer of the cylinder throughout, whether in stem or root. The continuity of the endodermis and other cortical tissues between stem

and root is also complete. The change from the epidermis of the stem to the piliferous layer of the root is, however, a sudden one.

e. Apical Development

We will now describe rather more fully how the development of the Wallflower plant takes place. We already know that the growing points, *i.e.* the regions where the formation of new organs and tissues goes on, lie at the extreme ends of the branches of both shoot and root. In every branch the base is the oldest, the apex the youngest part. It is at the apex, then, that we shall find development in progress.

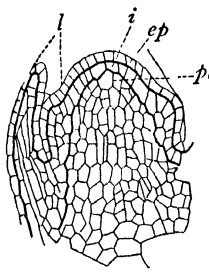


FIG. 32.—Growing point of a stem in longitudinal section. *l*, young leaves; *ep*, young epidermis, or dermatogen; *i*, periblem, or layer from which the cortex is developed; *pl*, plerome, which develops into the central cylinder. (After Douliot.) Magnified.

(*a*) *The growing point of the shoot.*—If we examine a longitudinal section passing exactly through the middle of a growing point, we find that the end of the stem has a nearly flat or slightly domed surface. If the section has passed through one or more of the very youngest leaves, we shall see that they arise as slight projections on the sides of the growing apex. Lower down, we come to rather more advanced leaves, which at first simply show an increase in size; while farther down still, their tissues begin to be differentiated.

Now, the growing point and the very youngest leaves consist entirely of thin-walled cells rich in cytoplasm, with relatively large nuclei. Such cells have already been described (p. 28). All these cells are in course of active growth and division, and therefore the tissue of the growing point is called *meristem* or *dividing tissue*. From this meristem all other tissues are derived. In favourable sections we can distinguish three distinct meristematic strata at the apex; the outermost of these is a single layer of cells, dividing exclusively by walls at right angles to the surface, and giving rise to the epidermis only. This is called the *dermatogen* (Fig. 32, *ep*). It extends not only over the growing point of the stem, but also over the young leaves, for the dermatogen forms the epidermis of the leaves as well as that of the stem. Next below the dermatogen we find a stratum which may be only one cell thick at the extreme apex, but which lower down divides by cell-walls parallel to the surface as well as by walls at right angles to it, and thus becomes several layers in thickness. This is the *periblem*, or young cortex (Fig. 32, *i*). Lastly, underneath this again, we find a group of meristematic cells which divide in all directions, and form the central cylinder of the stem, including the pericycle, vascular bundles, pith, etc. This last group is called the *plerome* (Fig. 32, *pl*).

The dermatogen is always a distinct layer. The periblem and plerome, however, often unite in a common layer of meristem at the extreme apex.

The vascular bundles begin to develop at some little distance from the apex. The outer part of the plerome divides up more actively than the rest, giving rise to a small-celled tissue. Within this zone certain strands of cells divide more frequently by longitudinal than by transverse walls, so that they come to consist of rather elongated cells. These constitute the *procambial strands*, each of which develops into a vascular bundle, as already described. The innermost elements of each strand thicken their walls and become the protoxylem, while the outermost are converted into the protophloëm. The successive development of the elements then goes on from within outwards in the xylem, and from without inwards in the phloëm. But, as it is an open bundle with which we are concerned, there is always a layer of cells left between wood and bast, which remains capable of dividing, and forms the cambium of the bundle, by means of which it can increase the number of its elements indefinitely.

Only the dermatogen and periblem take part in the formation of the leaves. To form a leaf, the outer layers of the periblem grow out, and divide by walls parallel to the surface, while the dermatogen follows their growth (see Fig. 32, *l*). The latter gives rise to the epidermis of the leaf only. All its other tissues—vascular bundles as well as mesophyll—are formed from the periblem. The plerome of the stem takes no part in the development of the leaf.[1]

[1] Most observers agree that this is the case. It has recently been stated, however, that the cells of the plerome grow out to form the leaf-trace bundle.

The growth of the leaf itself, unlike that of the stem, goes on chiefly at the base, the lower part of the leaf continuing to develop long after the apex is fully formed. We see that in each leaf-trace bundle that part which belongs to the stem is formed from the plerome, while that which belongs to the leaf may arise from the periblem. The part at the node where the vascular bundle bends out towards the leaf is generally the first to be formed. From this point the differentiation of the vascular tissue proceeds upwards into the leaf and downwards into the stem.

When a branch arises in the axil of a leaf, it is formed, like the leaf itself, entirely from the more external tissues. The branch is developed a little later than the leaf, and rather more layers of the periblem take part in forming it. But here again the plerome is said not to be concerned in the process.

(*b*) *The growing point and branching of the root.*—The root, like the shoot, forms its new tissues at the apex of each branch, but as the structures to be produced are different it is evident that the meristem which produces them must be different also. In roots there are no leaves to be formed, and, on the other hand, the root-cap has to be provided for. Hence arise the chief differences between the growing points of shoots and roots. It is obvious that we must here seek the meristem, not at the extreme end of the root, but inside the root-cap.

In a root like that of the Wallflower the meristem of the apex consists of three layers (see Fig. 33). The innermost forms the plerome, which here, as in

the stem, gives rise to the vascular cylinder. The next outer layer is the periblem, which develops into the cortex; the pericycle is formed from the outermost layer of the plerome, and the endodermis from the innermost layer of the periblem. So far there is no difference from the meristem of the shoot.

The external part of the meristem gives rise at once to the piliferous layer and to the root-cap We may call it the *calyptrogen*, or cap-forming layer. Its cells divide not only by walls at right angles to the surface, but also in the direction parallel to it. The cells which are thus cut off towards the outside of the calyptrogen go to form the root-cap, those cut off towards the inside form the piliferous layer, which always remains one cell thick.

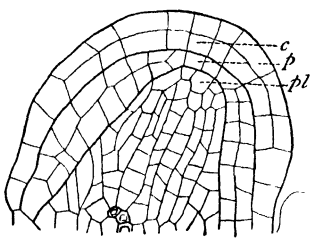


FIG. 33. — Young rootlet of *Sinapis* (allied to Wallflower) in longitudinal section. *c*, calyptrogen; *p*, periblem; *pl*, plerome. (After Van Tieghem.) Magnified about 250.

As regards the differentiation of the various tissues from the meristem, there are a few points to be noticed, though, on the whole, what has been said of the stem applies here also. The cells of the root-cap remain living for a time, and grow larger. The oldest of them, however, which lie farthest towards the outside, gradually die off, becoming partly converted into a slimy mucilage, which serves to diminish friction between the root-tip and the soil; they are replaced by new cells formed from the calyptrogen. The other tissue formed from the calyptrogen, namely,

the piliferous layer, is remarkable for the great growth in length of those of its cells which form the root-hairs, organs of which we have already learnt the high physiological importance. The development of the cortex calls for no remark.

The plerome here, as in the stem, gives rise to *procambial strands*, which in the root occupy much the greater part of the young vascular cylinder, as there is only a little *conjunctive parenchyma* between them, and no pith is present. In some plants, however, the root possesses a pith. The external part of the conjunctive parenchyma forms a single-layered pericycle, which extends all round the cylinder. In the root each procambial strand gives rise to xylem or to phloëm only.

The *branching of the root* is very characteristic of that organ, and quite different from that of the stem. All the branches arise *endogenously*—that is to say, they are formed from deep-seated tissues, and have to make their way through the external structures in order to reach the surface. In the Wallflower, and indeed in all Flowering Plants, the *pericycle* is the layer from which the rootlets are developed.

The position in which the branch-roots or rootlets are formed has a definite relation to the xylem. In the Wallflower and its nearest allies the rootlets usually form four rows, which are so placed that one lies a little to the right, and another a little to the left, of each of the two protoxylem strands of the parent root. Sometimes, in place of the four rows, there are only two, which are then situated exactly opposite the two protoxylem strands. The develop-

ment of the rootlets begins fairly early, but not so close to the apex as is the case with the appendages of the stem. It begins, however, before the central vessels of the xylem-plate have become lignified. A group of pericyclic cells, situated (in the more usual case) a little on one side of one of the protoxylem strands, begins to elongate radially, the middle cell elongating most. All these cells then divide by tangential walls. The inner cells thus cut off go to form the plerome of the rootlet (see Fig. 34, *pl*). The outer layer divides again (with the exception of the cells lying at the extreme edge of the group), and of the two layers thus formed the more internal gives rise to the periblem (*p*), while the outermost becomes the calyptrogen (*c*), producing the piliferous layer and root-cap. We thus have the three meristematic layers marked off from the first. They continue to grow and divide in the usual manner. The young rootlet grows out through the cortex of the parent root, the cells of which are not mechanically pushed aside, but are actually digested by the rootlet, and their substance absorbed by it as food (see Fig. 34, *d*). Eventually the piliferous layer is reached and absorbed, and then the tip of the rootlet becomes free and penetrates into the ground. We see that the origin of the branches of the root is just the converse of that of the leaves and branches of the stem. In the latter the tissues of the leaf or branch are formed from the dermatogen and periblem; it is doubtful whether the plerome takes any part in the process. In the root it is the plerome alone which forms the

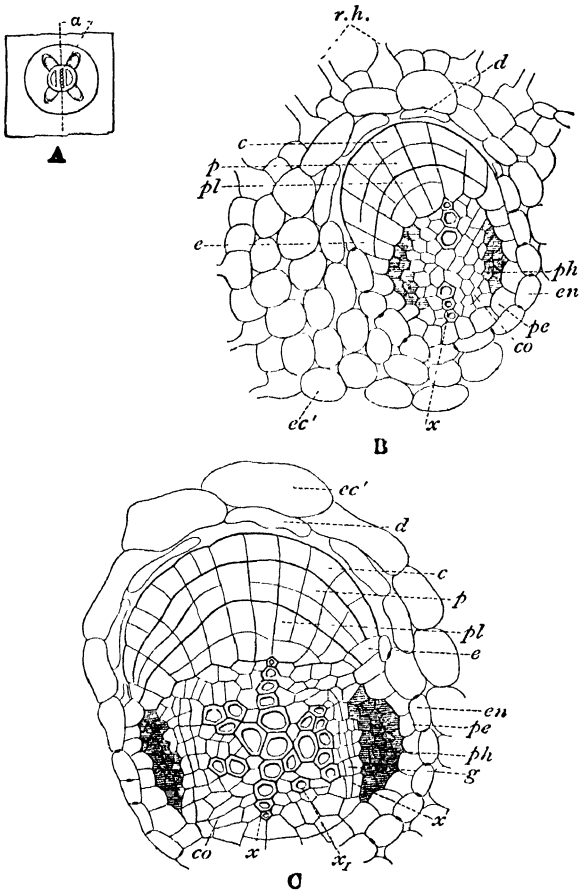


FIG. 34.—A, Diagrammatic transverse section of a diarch root, to show the position of rootlets. B and C, Transverse section of root of *Hesperis* (allied to Wallflower), to show a rootlet at two stages of development: *r.h*, root-hairs; *ec*, cortex; *d*, cells in process of absorption; *en*, endodermis; *pe*, pericycle; *co*, conjunctive tissue; *ph*, phloem; *g*, cambium; *x*, xylem; *c*, calyptrogen of rootlet; *p*, its periblem; *pl*, its plerome. (After Van Tieghem.) B and C magnified about 250.

branch. It is clear that the rootlet, owing to its endogenous origin, has the advantage of a more protected position from the first—a protection which it needs, as its delicate tissues would otherwise be exposed to injury by contact with the soil. The *endogenous mode of branching* is one of the most constant characters by which roots may be distinguished from stems.

f. Secondary Growth in Thickness

The stem and root of the Wallflower, like those of most members of the Class to which it belongs, go on increasing in thickness as long as the plant lives. This is due to the activity of the cambium, the origin of which, in the vascular bundles themselves, we have already described. It is impossible to draw a sharp line between procambium and cambium; for the latter, as we have seen, is simply the permanently active middle part of the procambial strand; but it is to be noticed that while, in the earlier stages of development, the cell-divisions in the procambium take place indiscriminately in all directions, after a time they become very regular, nearly all the new walls being formed in the tangential direction, *i.e.* parallel to a tangent drawn to the surface of the stem, while radial walls are formed at long intervals only. This regular tangential division is characteristic of the cambium as distinguished from the procambium (Fig. 21, *c*, p. 51).

The cambium of the bundle, then, goes on growing and dividing without limit; on its inner side it cuts off cells, which, after one or two further divisions,

gradually become converted into vessels, parenchyma, or fibres of the wood. In the same way the cells cut off on the outer side of the cambium divide once or twice, and then become sieve-tubes, companion-cells, or parenchyma of the bast. The amount of wood formed on the inside is much greater than the amount of bast formed on the outside of the cambium. Now, this production of new xylem and phloëm only adds to the size of each individual vascular bundle. In an old Wallflower stem, however, we find that the vascular bundles are no longer isolated, but there is a thick continuous zone of wood, surrounded by a narrower zone of bast. How is this brought about? It depends on the fact that the cambium does not remain isolated within each bundle, but becomes united to form a complete ring all round the central cylinder of the stem.

When the stem is quite young, we find the vascular bundles separated from one another by radial bands of conjunctive parenchyma—the primary medullary rays (see p. 48, Fig. 20, *if*). There is already an active cambial layer between the xylem and phloëm of each bundle, and soon the infection of division spreads to the neighbouring cells of the ray parenchyma, which also begin to divide up by tangential walls. Thus a layer of cambium is formed across each primary ray, joining the cambium of the bundles on either side, and so the whole central cylinder comes to be encircled by a zone of actively dividing cells, producing new wood internally and new bast externally. The cambium within the vascular bundles, derived from the original

procambial strand, is called the *fascicular* cambium; that between the bundles, formed by division of the cells of a primary medullary ray is the *interfascicular* cambium.

The interfascicular wood, *i.e.* that formed by the parts of the cambium between the bundles, consists at first chiefly of fibrous cells and parenchyma, but farther to the outside vessels are formed here also. The limits between the original bundles can, however, always be traced, for the cambium produces a radial band of parenchymatous tissue two or more cells thick, which extends right through from pith to pericycle; this is called a *principal medullary ray* (see Fig. 35). It corresponds in position with a primary ray, and forms, as it were, the continuation of it, but is much narrower, for the cambium only forms the ray parenchyma just opposite the middle of the primary ray. The cells of the ray are short, with square ends; their walls are thick and pitted (see Fig. 36, *mr*); they form starch in summer, and are easily distinguished by their shape from any other cells of the wood. The part of the ray which is formed on the outside of the cambium broadens out, its cells becoming both larger and more numerous. Between the principal medullary rays there are shorter secondary ones (Fig. 35, *s.m.r*), which are started by the cambium after growth in thickness has gone on for some time, and which therefore do not extend either inwards to the pith or outwards to the pericycle. The secondary as well as the principal rays broaden out in the phloëm. As the wood constantly increases in thickness, it is evident that all the tissue outside it

must become stretched. This stretching is partly provided for by the tangential expansion, followed by radial division, of the cells forming the phloëm-rays, so that the phloëm itself does not get distorted.

The cells of the secondary wood and bast are essen-

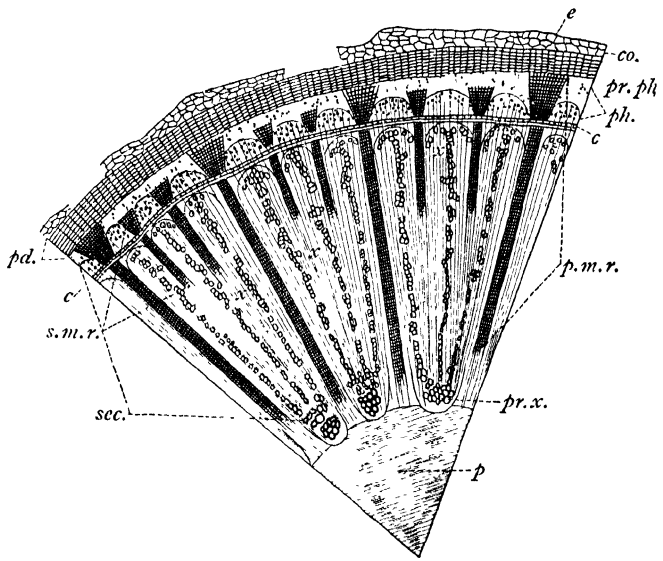


FIG. 35.—Diagrammatic transverse section of part of an old stem of Wallflower, including three of the original bundles. *e*, epidermis; *co*, cortex; *pd*, periderm; *pr.ph*, primary phloëm; *ph*, phloëm; *c*, cambium; *sec*, secondary tissues; *pr.x*, primary xylem; *p.m.r*, a principal medullary ray; *s.m.r*, a secondary medullary ray; *p*, pith. Magnified about 20. (R. S.)

tially like those of the primary tissues. The chief forms of xylem-elements are shown in Fig. 36.

The cambial cells are elongated prisms with inclined ends (see Fig. 22, p. 52). Where a medullary ray is

being formed, however, the cambium has short, square-ended cells; and when a new secondary ray is to be started, the cambial cells first divide up by transverse walls, so that in this case the form of the cambial cells

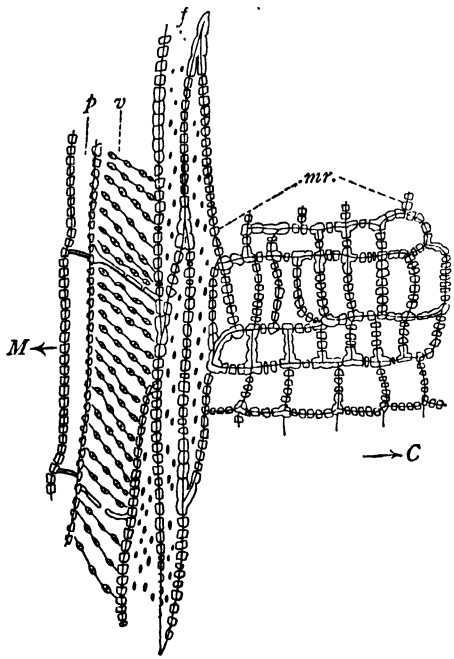


FIG. 36.—Part of a radial section through the secondary wood of Wallflower. *p*, xylem-parenchyma; *v*, vessel; *f*, fibrous cell; *mr*, medullary ray. The arrows *M* and *C* point respectively towards pith and cortex. Magnified 220. (R. S.)

is similar to that of the elements which they produce. This, however, does not hold good elsewhere, for the vessels and fibres of the wood undergo considerable

changes during their development from the cambium. The vessels have a much greater diameter than the cambial cells, while the fibres are more elongated.

If we think the matter over carefully, we shall see that these changes of dimensions in particular cells cannot go on without some disturbance of the original arrangement of the cells. Take a vessel, for instance: as its diameter increases, it has to find room for itself among the surrounding parenchymatous and other cells which do not grow much in diameter. To do this it has to displace its neighbours, and eventually it comes into contact with many more cells than it touched when first formed from the cambium.

Next consider the excessive growth in length of the fibrous cells; each of these when full grown is about twice as long as it was in the cambial condition. In attaining its full length it has to insert its pointed growing ends between its neighbours, and as they, if they are fibrous cells, are all doing the same thing, the ends of these cells have to grow past each other (see Fig. 36, *f*). All this may happen in a part of the stem which has long ceased to grow in length, so that all the room required must be found by the mutual displacements of the growing cells. To all changes of this kind in which developing cells grow past each other, whether in transverse or longitudinal direction, the name of *sliding growth* is applied. The meaning of the term is, that the walls of these cells slide upon each other as they grow.

g. Periderm

We know that the young stem is covered by the epidermis; the old stem, however, is coated by a greyish bark, much thicker and harder than the epidermis; this bark splits lengthways here and there; as the stem grows thicker, the cracks widen and expose the softer tissues below, until these too become coated over by new bark.

If we examine the bark of the Wallflower microscopically, we find that its outer layers consist of the epidermis and the whole of the cortex in a dried and withered condition (see Fig. 35, *e* and *co*). The inner part of the bark is formed of closely-packed cells, which are arranged in regular radial rows, and which have their walls corky or *suberised.* These walls have undergone a similar change to the cuticularisation of the outer epidermal cell-wall, and so the corky tissue has become almost impermeable to water or water vapour, just as is the case with the ordinary corks used in bottles, which are made of this tissue, obtained from the Cork Oak (*Quercus suber*). The cortex, which lies outside this corky zone, is thus completely cut off from all supplies of water and food from within, and consequently withers and dies. Now we will see how the bark is formed.

The pericycle, which encloses the whole vascular cylinder, is at first one cell thick. Soon after secondary thickening has begun, however, its cells divide, so that it becomes three or four cells in thickness. These divisions take place rather irregularly

Then the outermost layer of the pericycle begins to divide with great regularity by tangential walls (see Fig. 37, *pd*), so that a cambial layer is formed, which, like the true cambium, extends all round the stem. This is called *cork cambium* or *phellogen*. It produces cells, both on its inner and outer side. Those cut off towards the inside retain their living contents, and have rather thick cellulose walls. There are several layers of these cells in the Wallflower; together they constitute the *phelloderm*. The cells cut off on the outside of the phellogen have their walls suberised and their contents disappear. These cells form the *cork*.

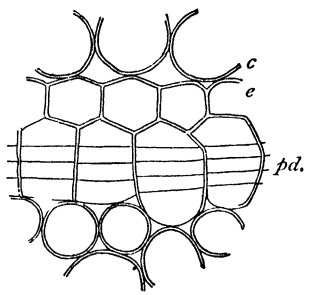


FIG. 37.—Part of a transverse section of the stem of Wallflower, to show the outermost layer of the pericycle dividing up to form the periderm. *c*, cortical cells; *e*, endodermis; *pd*, phellogen, arising by division of pericyclic cells. Magnified 460. (R. S.)

The whole of this secondary tissue, including phelloderm, phellogen, and cork, is called the *periderm*. The word *bark* is applied to everything outside the phellogen, and so here it includes the corky layers, together with the endodermis and the rest of the cortex and the epidermis. The bark consists entirely of dead tissues, for the corky walls allow of no absorption of water or food-materials. It is, however, of great importance as a protection to the living tissues within. Almost all plants with secondary growth in thickness form periderm and bark through the activity of a phellogen, which, however, does not

always arise from the pericycle. The bark of our trees and large shrubs arises essentially in the same way as that of the Wallflower, though there are many differences of detail.[1]

h. Secondary Thickening in the Root

The root, like the stem, grows indefinitely in thickness, owing to the formation of new tissues from a cambium. This secondary growth begins very early in the root, just after the stage shown in transverse section in Fig. 28, so that in the older roots much the greater part of the tissue is of cambial origin. The first formation of the cambium in the root is rather different from that in the stem, owing to the different arrangement of the primary tissues. It has already been mentioned that the two phloëm groups are separated from the xylem by parenchymatous cells belonging to the conjunctive tissue. It is in these cells that the tangential divisions begin. The cambium, consequently, at first forms two bands of actively dividing cells, lying on either side of the xylem-plate and immediately within the two phloëm groups (see p. 89, Fig. 34, *C*, *g*). These cells give rise to new xylem on the inside and new phloëm on the outside in the usual way, but the cambium does not as yet form a complete ring. It is completed in this way. The pericycle, which was at first a single layer of cells, divides and becomes two or more cells in thickness, at least at the places opposite the two protoxylem

[1] In popular language the word "bark" is commonly used to denote all tissues outside the cambium, and thus includes the phloëm. This wider use of the term is adopted in some botanical works.

groups. The innermost of these pericyclic cells, *i.e.* those lying next the protoxylem, now undergo regular tangential divisions, and so form the continuation of the cambium round the ends of the xylem-plate. It is a constant rule in plants of the class to which the Wallflower belongs, as well as in plants of the Fir kind, which belong to a different Class (cf. Fig. 104, p. 254, and Fig. 106, p. 258), that the formation of the cambium in the root begins by division of the conjunctive cells inside the phloëm-groups, and is completed by division of the pericyclic cells outside the xylem-groups. Thus the cambium (as seen in transverse section) cannot at first form a perfect circle, for it has a depression opposite each phloëm bundle; but just at these places the cambium starts its work earliest, and is for a time most active, so that the inequalities soon become equalised, and we have a circular zone of actively dividing cells just as in the stem. When once started, there is nothing peculiar about the cambium of the root; it forms internal wood and external bast just as it does in the stem, but as in this root there is no pith, it is evident there can be no principal medullary rays. One point deserves special attention: the primary xylem of the root develops, as we have seen, from without inwards; the secondary xylem is formed by the cambium from within outwards, so that in roots we have a sharp distinction between *centripetal* primary and *centrifugal* secondary wood, whereas in the stem all the wood arises centrifugally. However old the Wallflower root may be, we can always tell its transverse section from that of the stem, for in the middle, instead of the pith, we find the little diarch xylem-plate unaltered. In

the roots of other plants of the same class there are often more than two groups of xylem, and a pith may even be present; still, if we can once make out the position of the protoxylem elements, we can always be certain whether it is a root or a stem with which we have to do.

Only very young parts of the root retain their root-hairs, and absorb food from the soil. The older parts soon lose their hairs, cease to be absorptive, and now serve only to conduct the food, which the younger part of the root has taken up, towards the stem. These older parts of the root acquire a covering of periderm. The pericycle divides up to form a phellogen, which produces phelloderm internally and corky layers externally, just as in the stem.[1] It is from the outer layer of the pericycle (where it is double) that the phellogen arises. We now see that the pericycle in these roots is an extremely important layer, being the seat of three distinct new formations—

(1) Lateral roots.
(2) Cambium (in part).
(3) Phellogen.

In consequence of the formation of cork by the phellogen, all the external tissues, from the endodermis outwards, wither away, so that the older roots consist entirely of the central cylinder surrounded by periderm. A curious effect of this throwing off of the cortex, which takes place very early in roots, is that

[1] In the case of roots the origin of the phellogen from the pericycle is the rule, while in stems it is the exception.

they appear thinner, after secondary growth in thickness has begun, than they did before. This is because the root at first loses more by the death of its external tissues than it gains by secondary growth. The loss, however, is soon made good.

Now let us consider what purpose all this secondary formation of new tissues serves. So long as a plant like the Wallflower lives, it keeps putting out new branches; every new branch bears a number of leaves, and so the older the plant grows the greater is the total surface of its foliage, in spite of the loss of old leaves. Now the leaves perform two main functions: they give off water vapour through their stomata, and thus keep up the ascending current of sap from the roots; and also they take up food from the air, namely, the carbon which they obtain by the decomposition of carbon dioxide. Therefore the greater the leaf-surface, the greater will be the amount of water which has to pass up the stem from the roots, and the greater also will be the amount of assimilated food which has to be conveyed away from the leaves to the growing parts. Consequently, as the leaf-surface increases, it is necessary that the amount of conducting tissue should increase also, and this applies both to the wood, which conducts the sap from the roots to the leaves, and to the bast, which conducts the assimilated foods from the leaves to the seats of growth. This increase is provided by the activity of the cambium, and while this is going on the absorptive surface of the root is also increasing. The root branches again and again, and the number of young

roots that are able to take up food from the soil is constantly becoming greater.

Thus we see how the growth of all the vegetative organs of the plant works together. As the transpiring and assimilating surface of the leaves increases, the amount of conducting tissue in the stem and older roots increases at an equal rate, while at the same time the branching of the younger roots provides for the greater demands on their absorptive capacity.

Secondary growth in thickness is important in other ways also: as the branching of the shoot goes on, it is obvious that the stem has an ever-increasing load to bear, due not merely to the increased weight, but also to the greater leverage of the spreading branches. Hence the necessity for increased mechanical strength, which is provided for by the formation of additional wood, and especially of new fibrous elements, from the cambium.

Lastly, the constant formation of new tissues has the further advantage that old elements which have become past work are replaced by young and active ones. This applies especially to the phloëm, in which it is generally the newer layers which are alone active. This point, however, is not so important in the Wallflower as in some other plants, especially trees, in which the duration of life is longer. Secondary growth, then, has three main functions: to increase the conducting tissues, to increase the mechanical tissues, and to replace old elements by young ones.

III. *INTERNAL STRUCTURE AND DEVELOPMENT OF THE REPRODUCTIVE ORGANS*

We use the term "reproductive organs" here in a wide sense, to include all the parts of the flower, although many of these are only of indirect service in reproducing the plant. We do so because the sole function of these organs is to form a sexually produced embryo or young plant, and to send it into the world as well equipped as possible for its future life. The floral organs are only of service in so far as they contribute to this end.

We have already learnt the general arrangement and outward appearance of the parts of the flower (see p. 18); we will now consider the order and method of their development.

a. Development of the Flower

The very young flower-bud arises from the stem as a rounded outgrowth, which soon acquires a short stalk (see Fig. 38). The calyx is the first of the floral organs to appear. The anterior sepal takes the lead, appearing as a crescent-shaped ridge of tissue (see Fig. 38, A, s^a); next the two lateral sepals (s^l) appear together, and lastly the posterior one, which lies next the main flower-stalk (B, s^p) (see also diagram, Fig. 13, p. 23). When the calyx has started its growth, the corolla begins to develop. All the four petals show themselves simultaneously, arising as small papillæ immediately within the calyx at the points corresponding to the spaces between the sepals (see Fig. 38, C, p^a and p^p).

The petals have no sooner appeared than their growth ceases for a time. Hence we shall find that the next inner whorl, that of the stamens, soon overtakes them.

The stamens appear in the same order as the sepals, opposite which they arise. First an outgrowth is formed opposite the anterior sepal (Fig. 38, D, st^a). It immediately forks into two, and gives rise to the anterior pair of long stamens (E, et^a). Next two papillæ are formed opposite the two lateral sepals. These develop into the two short lateral stamens (D and E, st^l). Finally a posterior papilla is formed, which like the anterior one immediately branches and produces the posterior pair of long stamens (D and E, st^p and *et*).

The pistil is the last part of the flower to be formed. The two carpels appear as two slightly elevated ridges opposite the lateral sepals; they are only distinct at their very first origin. A zone of tissue underneath their insertion begins to grow up immediately, carrying the carpels up with it, and forming a tubular column in the centre of the flower, on the upper edge of which the original carpels can scarcely be distinguished (Fig. 38, E, *cp*). On the inside of the carpellary tube two longitudinal ridges arise; the position of these ridges is posterior and anterior, *i.e.* they come midway between the centre-lines of the two carpels (F and G). These ridges are the *placentas*, on which the ovules or future seeds are borne. Two elevations soon appear on the edge of the carpellary tube just above the placentas. These elevations become the stigmas (F and H, *sg*), and ultimately close in over the top of the

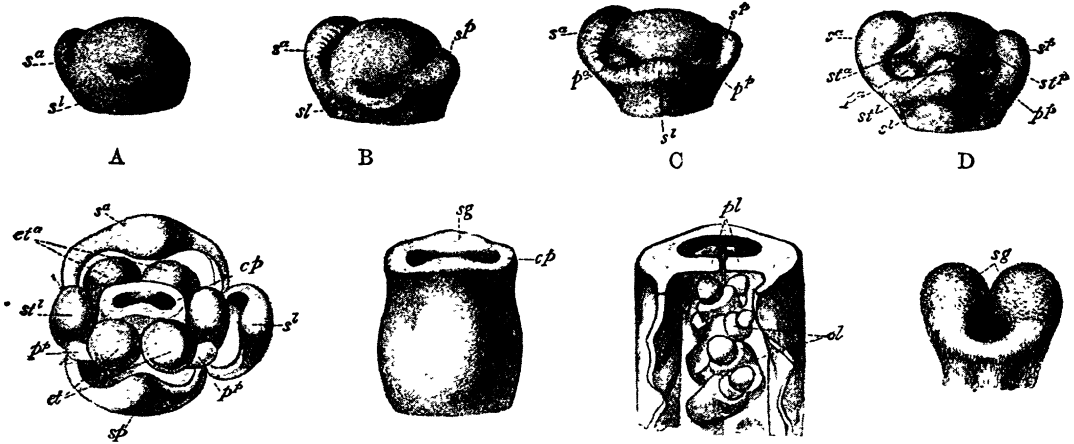


FIG. 38.—Development of the flower in *Cheiranthus*. A, Very young flower-bud, seen from the side: s^a, anterior sepal; s^l, a lateral sepal. B, Slightly older: s^p, posterior sepal. C, Older: p^a, one of the anterior petals; p^p, one of the posterior petals. D, Older: st^l, a lateral stamen; st^a and st^p, stamens of the anterior and posterior pairs. E, Older bud, seen obliquely from above: ct^a, anterior pair of stamens; *ct*, posterior pair of stamens; st^l, a lateral stamen; *cp*, carpellary tube. F, Pistil somewhat more advanced: *cp*, centre-line of carpels; *sg*, centre-line of stigmatic lobes. G, Older pistil, partly in section: *pl*, placentar outgrowth, forming the septum; *ol*, ovules. H, Young stigma: *sg*, stigmatic lobes. Magnified. (After Payer.)

tube, which now forms the cavity of the ovary (see Fig. 38, H). We see, then, how it is that the position of the stigmas is alternate with that of the carpels (see Figs. 10, 11, 12, and 13, pp. 20–23). The septum appears rather late, after the development of the ovules has begun (Fig. 38, G, *pl*). Each placenta grows out between the rows of ovules; the two projecting walls thus formed at last meet in the middle to form the septum, dividing the cavity into two. The honey-glands, which lie at the base of the two shorter lateral stamens, arise very late in the development of the flower, when all the more important organs are well advanced.

All floral leaves arise like other leaves, by the growth and division of the more external cells of the growing point, namely, the dermatogen and periblem.

b. Structure of the Floral Envelopes

We will now consider more fully the structure of the various organs of the flower, and the respective parts which they play in the process of reproduction. We will first consider the structure of a sepal. The *sepals* form the outer protective covering of a flower while it is still a bud. When the flower opens, the function of the calyx in the Wallflower is almost at an end.

Of all the floral organs the sepals most resemble foliage-leaves. They are, in fact, merely leaves of simplified structure, having less complex functions to perform than the vegetative leaves.

The sepal has a similar bundle-system to that of

an ordinary foliage-leaf, but with simpler ramifications. In each bundle the xylem and phloëm are in the usual position, the xylem being placed on the upper side, *i.e.* on the side turned towards the middle of the flower, and the phloëm on the lower or outer side. The mesophyll is of uniform parenchymatous structure throughout, showing no differentiation between palisade and spongy tissue. The cells contain numerous plastids corresponding to the chlorophyll granules, but little or no chlorophyll is present. The dark colour of the sepal is due to purple cell-sap, which is present in the more superficial layers on both the upper and lower sides of the sepal. It is most abundant towards the lower surface, and especially in the hypodermal layer, though it also occurs in the epidermis. Stomata are fairly numerous on both surfaces of the sepal. Hairs of the structure already described and figured (see Figs. 26, 27, and 43) are produced on the lower or outer surface only. There is reason to believe that they serve to protect the young flower-bud from the attacks of slugs.

The *petals*, which form the next floral whorl, are in many respects of very different structure. The petals are at first very slow in their development, and become mature rather suddenly, shortly before the flower is ready to open. They are transitory structures; they have no protective function, nor do they take any direct part in fertilisation or the production of the embryo, but they are none the less important. The Wallflower is in a great degree dependent on the visits of insects for its fertilisation. The function of

the petals is to render the flower conspicuous, and thus to help in attracting insect visitors. Hence, it is generally the corolla which constitutes the chief beauty of the flower in our own eyes. Its business is to be showy. Each of the petals has a vascular system; its bundles, though slender, are of normal structure, with xylem above and phloëm below. The mesophyll consists entirely of spongy parenchyma without chlorophyll. The epidermal cells of both surfaces contain very numerous yellow chromoplasts —that is, protoplasmic bodies like chlorophyll granules, but containing a yellow pigment instead of chlorophyll. To these the yellow colour of the petals is due. In cultivated Wallflowers a purple cell-sap is also present, chiefly in the lower epidermis. To the combination of the colours of the yellow chromoplastids and of the purple cell-sap the flower owes those beautiful red-brown shades which we know so well. The wild Wallflower generally has the chromoplastids only, and so its petals are simply yellow.

There are no stomata on either surface of the petal. The epidermis is not smooth, but its cells all grow out into short hairs or papillæ, which are narrower and more prominent on the upper surface of the petal. They give it a peculiar velvety gloss, owing to the varying way in which they reflect the light, and this effect is perhaps enhanced by the fact that the cell-walls of the papillæ are delicately ridged.

The well-known pleasant scent of the Wallflower comes from the corolla. This scent is probably of importance as helping to attract insect guests.

c. Stamens

The six stamens together constitute the *andrœcium*, or fertilising apparatus of the flower. Each stamen, as we already know, consists of two parts—a stalk or filament, and an anther borne upon it. The stamens, like the other floral organs, are known by their development to be leaves, but their vegetative structure is much simplified in comparison with a foliage-leaf, or even with a sepal or petal. We regard them as much modified leaves, which have no vegetative functions to perform. The filament is traversed by two vascular bundles, having two small xylem groups turned towards the inner surface, and two larger united phloëm groups on the outer side. The vascular tissue is surrounded by an endodermis. The mesophyll is of uniform structure all through. The epidermis of the filament has neither hairs nor stomata, but the latter occur on the anther. The filament tapers at the top, and is attached to the anther by a narrow neck. The anther may be compared to the blade of an ordinary leaf, but it shows little trace of the structure of a vegetative lamina, for its functions are entirely reproductive. It is, however, traversed by a midrib (the connective), which forms a direct prolongation of the filament. The connective has a single vascular bundle, which is continuous with the two bundles of the filament (see Fig. 39, *v.b*).

The anther, when nearly ripe, is divided lengthways into two halves or lobes, with the connective between them (see Fig. 39, and compare Figs. 9, 10, and 11, pp. 19–21).

Each lobe of the anther consists of two compartments, called the *pollen-sacs*, so that there are four of these pollen-sacs altogether, running lengthways of the anther, parallel to the connective. Their arrangement, as seen in transverse section, is shown in Fig. 39. When ripe, each pollen-sac contains an immense number of isolated cells, the *pollen-grains*, which are set free by the

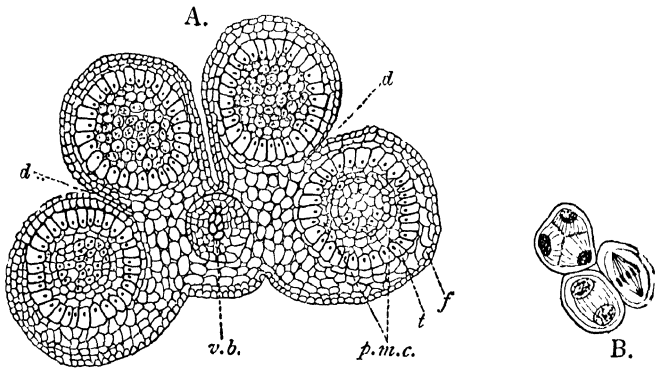


FIG. 39.—A, Transverse section through a young anther of Wallflower, at the stage when the pollen mother-cells are dividing. Observe the four pollen-sacs and the connective. *v.b*, vascular bundle of connective; *f*, hypodermal layer, which will become the fibrous layer; *t*, tapetum of radially elongated cells; *p.m.c*, mass of pollen mother-cells, derived from archesporium of the pollen-sac; *d*, places where the anther will dehisce. Magnified 110. B, Three pollen mother-cells from a pollen-sac in A, showing three stages of division. Magnified about 450. (R. S.) (Cf. Fig. 10, *st*, p. 20.)

bursting or dehiscence of the anther. The anther bursts by two longitudinal cracks, coinciding with the partition between the two pollen-sacs of each lobe of the anther (see Fig. 40).

The outer wall of the sacs is ruptured along this

line, and at the same time the partition separating the sacs is broken down (see Fig. 40, *w*), so that a single opening serves for the escape of the pollen from each pair of pollen-sacs. At the time of dehiscence, therefore, the anther appears to have only two cavities, and we have to go back to unopened anthers to find the four pollen-sacs intact.

We see, then, that the stamen is a modified leaf,

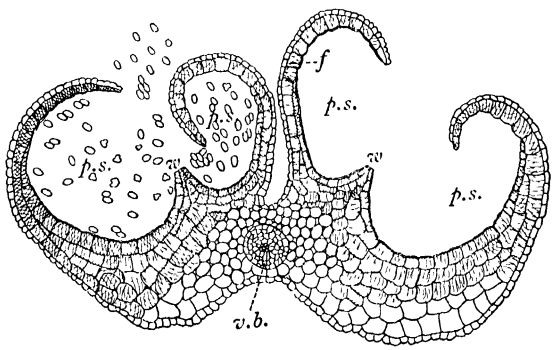


FIG. 40.—Transverse section of ripe anther of Wallflower, after dehiscence. Observe that the two pollen-sacs on each side have now opened into each other by the breaking down of the wall *w* between them. *v.b*, vascular bundle of connective; *p.s*, the four original pollen-sacs; *f*, fibrous layer. Magnified 44. (R. S.)

bearing four pollen-sacs, which produce in their interior numerous pollen-grains. It will now be well to trace the development of the pollen-sacs, and of the pollen which they contain.

The anther is the first part of the stamen to be developed, so that in a moderately young stamen we find the anther almost full-grown while the filament

is still quite short. If we cut a very young anther across, we find that the transverse section is nearly oblong, with rounded corners (Fig. 41, A).

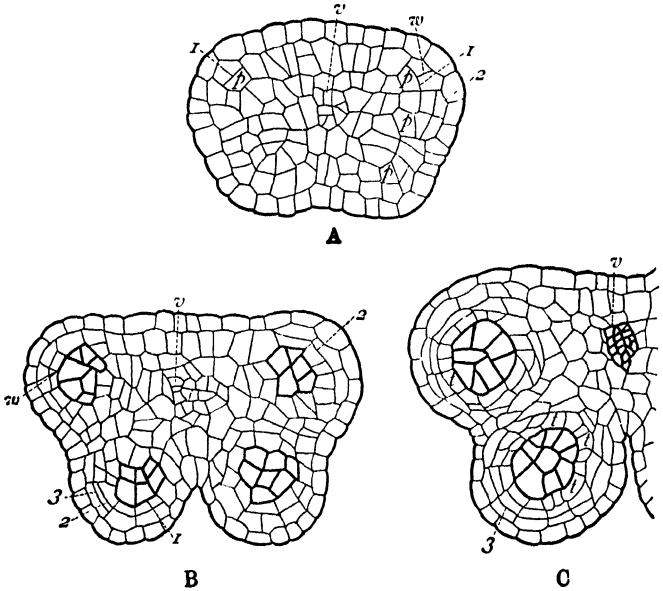


FIG. 41.—A, Transverse section of very young anther. *v*, young vascular bundle; *p*, *p*, pollen-sac initial cells which divide to give rise to archesporium and cells of wall, *w*. B and C, More advanced stages of the same. The cells with dark outlines belong to the four archesporia. The numbers 1, 2, and 3 refer to the order in which the cell-walls are formed. *t*, tapetum. (After Warming). Magnified about 200. These figures are reversed in position as compared with Fig. 39.

At each of the four corners two or three of the cells lying next below the epidermis divide by walls parallel to the surface (see Fig. 41, A, *p*). The inner

cells produced by this division form what is called the *archesporium*, *i.e.* the layer from which the *spores*, here called the pollen-grains,[1] ultimately arise. Each archesporium thus consists at first of a single strand or layer of cells running the whole length of the anther. The archesporial cells grow and divide up in all directions, and we soon have, in place of the original layer, a solid cylindrical column of tissue, consisting of large cells (see Fig. 41, B and C), which are densely filled with protoplasm, and have large nuclei. In the meantime the cells immediately outside the archesporium have undergone several divisions, so that the wall of the pollen-sac becomes about four cells thick (see Fig. 41, A, B, and C), including the epidermis, which does not itself divide. The cells which are actually in contact with the archesporium become elongated radially, and form a well-marked internal lining to each pollen-sac, called the *tapetum* (see Figs. 39 A, and 41 C, *t*). The tapetum extends all round the sac. Its cells are at first rich in protoplasm. The function of this layer is to feed the developing pollen-grains, by which it is entirely used up.

To return to the archesporium: after its cells have divided a great many times, the divisions cease for a while, the pollen-sac continues growing, its cavity becomes more roomy, and so the cells derived from the archesporium become isolated from one another and round off their corners (see Fig. 39, A). These cells now bear the name of the *pollen mother-cells*, because each of them divides up into four pollen-grains. The division takes place as follows: at the time when

[1] See Part II., *Flowerless Plants*, pp. 18 and 31.

the mother-cells begin to be isolated, the nucleus in each divides into two, and the two daughter-nuclei at once divide again, so that there are four nuclei in the mother-cell (see Fig. 39, B). New cell-walls are formed between the nuclei, and the mother-cell is thus divided into four distinct cells, each with its own nucleus. These four daughter-cells are arranged like four cannon-balls in a heap, the whole group having roughly the form of a four-sided pyramid or a tetrahedron.[1] Each daughter-cell next forms from its protoplasm a new cell-wall of its own. The wall of the mother-cell is dissolved, and the four pollen-grains are set free. The cavity of each pollen-sac is now filled with a host of free pollen-grains, four times as numerous as the original mother-cells. The grains are at first immersed in a half-fluid substance derived from the protoplasm of the tapetal cells, which break down during the formation of the pollen. This substance is soon used up by the pollen-grains to complete their growth.

The ripe pollen-grain is somewhat oval in shape. Its wall is considerably thickened, but there are three thinner bands, indicated externally by shallow grooves, which run lengthways of the grain. The pollen-grain in Fig. 42 is shown as if in cross-section, so that it appears round, with three depressions, and we see the three thin places in its wall at the depressed points. The rest of the wall is thick and cuticularised, except a delicate inner layer of cellulose.

[1] Hence only three are seen in one plane. See the mother-cell at the top of Fig. 39, B.

The pollen-grain at first, like most other cells, has a single nucleus. This nucleus divides while the grain is ripening, and one of the two daughter-nuclei divides again. Thus in the mature pollen-grain there are three nuclei, one of which is larger than the other two; the two smaller nuclei have arisen from the second division. From observations on other plants which are more favourable for examination than the Wallflower, it is probable that the protoplasm around each of the smaller nuclei forms a distinct cell, so that the mature pollen-grain thus consists of three cells. In many other plants the pollen-grain has only two cells at this stage (cf. the Lily, p. 178, Fig. 80).



FIG. 42. — A single pollen-grain of the Wallflower, showing the three thin places in the wall, at any one of which the pollen-tube may subsequently grow out. Observe the three nuclei, of which the largest is vegetative and the two smaller are generative. Magnified about 450. (R. S.)

The two layers of cells next outside the tapetum, like it, become absorbed. One of them often disappears even before the tapetum itself, as shown in Fig. 39, A. When the anther is ripe, the wall of each of the four pollen-sacs consists on its free outer side of one or two layers besides the epidermis. These persistent layers are distinguished by a strongly-marked spiral or netted thickening on their membranes. These cells form the *fibrous layer* (see Fig. 40, *f*). It completely surrounds each pollen-sac, except at the point just opposite the partition which separates the two pollen-sacs in the same lobe. Here the fibrous layer is interrupted by one or two thin-

walled cells. It is thinnest (one cell thick) next the partition, and attains its maximum thickness (about five cells) on the side towards the connective (Fig. 40) This layer is of great importance in the dehiscence of the anther. It is owing to the hygroscopic contraction of the fibrous layer, when the ripe anther is getting dry, that the wall is ruptured and dehiscence takes place. If the anther is kept from drying, as sometimes happens in very wet weather, dehiscence may fail to take place.

d. The Pistil

The development of the pistil has already been shortly described. The tissue of the carpellary tube is traversed by several vascular bundles, the largest of which are placed opposite the septum. The external epidermis is thickly clothed with hairs of the usual structure; there are a few stomata. The pistil terminates above in the stigma, the two lobes of which are rough on their inner side, with long papillæ, which, as we shall see presently, serve to catch the pollen-grains.

The ovary contains the *ovules*, or young seeds (see Figs. 10, 11, pp. 20, 21; Fig. 38, G, p. 105). They are numerous, and grow in four rows, two rows to each compartment, on the placentas.

Each ovule is attached to the placenta by a stalk, the *funicle*.

The body of the ovule consists of a central mass of tissue, the *nucellus*,[1] continuous with the funicle, and

[1] In the ovule of Wallflower, when ready for fertilisation, the nucellus is only represented by the embryo-sac (*e*) and a small mass of tissue at its base (*n*), Fig. 43.

of two coats, the *integuments*, which arise from the lower part of the nucellus and enclose it, leaving only a narrow passage, the *micropyle*, leading down to the free end of the nucellus. The funicle contains

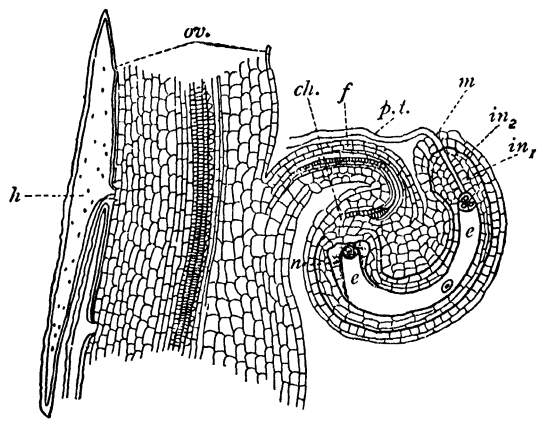


FIG. 43.—Longitudinal section through an ovule and part of the ovary wall of Wallflower. *ov*, ovary wall; *h*, a hair; *f*, funicle of ovule; *ch*, chalaza; *n*, nucellus (which is only persistent at the base); in_1, inner integument; in_2, outer integument; *m*, micropyle; *e*, *e*, embryo-sac; *p.t.*, pollen-tube, entering micropyle. Magnified about 50. (R. S.)

a vascular bundle, branching off from the bundle-system of the ovary. The bundle terminates at the base of the nucellus (see Fig. 43, *ch*). The base of the ovule, where the integuments spring from the nucellus, is called the *chalaza*. All these parts, except the vascular bundle, consist of delicate parenchyma.

In the nucellus is a long cell, the *embryo-sac* (see Fig. 43, *e*), which is much larger than its neighbours, and contains in its interior a number of smaller cells. One of these, situated at the end of the sac towards the micropyle, is the *ovum* (Fig. 44, 8 and 9, *o*), the most important part of the whole structure, because when fertilised it develops into the *embryo*, or young plant of the next generation.

The development of the ovule will now be traced in the Shepherd's Purse (*Capsella Bursa-pastoris*), a common weed allied to the Wallflower, which will show us all the essential points.

Each ovule arises as an outgrowth from the placenta. Several cells belonging both to the epidermis and to the next lower layer, take part in its formation. This outgrowth is the nucellus of the future ovule. When it has attained the form shown in Fig. 44, 1, that cell of the middle row which lies next below the epidermis (*e.m.* in the Fig.) begins to be distinguished from its neighbours by its larger size and more abundant protoplasm. It is termed the *archesporium* of the ovule. It divides by two transverse walls into a row of three cells (see Fig. 44, 2 and 3). The lowest of the three becomes the embryo-sac (Fig. 44, 3, *e*). The two sister-cells above it become completely destroyed (see Fig. 44, 4), and are, in fact, devoured by the growing embryo-sac.

In the meantime the integuments have begun to form; the inner one arises first, growing out as a ring of tissue at the base of the nucellus, and forming a sheath around it, which soon projects beyond its free end and almost encloses it (see Fig. 43, in_1). The outer integument next appears in like manner, just below the inner one, which it soon overtakes by its more rapid growth (see Fig. 43, in_2). Ultimately the outer integument closes in over the inner, leaving only the narrow micropyle as a passage leading through them both to the nucellus (Fig. 43, *m*). In the meantime the funicle has been formed by the growth and division of the cells at the base of the ovule (Fig. 43, *f*).

Returning to the embryo-sac, we find that it not only absorbs its sister-cells, but, as it continues to grow, soon attacks the epidermis of the nucellus. This also is quickly digested, so that only the basal part of the nucellus, lying below the embryo-sac, remains (Fig. 44, 4 and 5; Fig. 43, *n*), while the sides and top of the sac come into direct contact with the inner integument (see Fig. 43).

While these changes are going on, the nucleus of the embryo-sac divides, and the two daughter-nuclei travel, one to each end (see Fig. 44, 5). Each divides again (see Fig. 44, 6), and the four nuclei thus formed divide once more, so that there are now eight nuclei altogether in the embryo-sac, four near each end. As yet the nuclei only have divided, so that all the eight lie free in the cytoplasm of the sac. Now, however, the cytoplasm at each end divides into three

distinct cells, each surrounding a nucleus. Thus we have six cells in the embryo-sac, three at each end, and also two free nuclei, which lie in the undivided cytoplasm which occupies all the middle part of the sac (see Fig. 44, 7). The three cells at the end towards the micropyle form what is called the *egg-apparatus* (Fig. 44, 7, *e.a*). Of these three, the one farthest from the micropyle is the ovum (Fig. 44, 8, *o*). The two others are termed the *synergidæ* (*s*, *s*), because they co-operate, as we shall see, in bringing about the fertilisation of the ovum. The three cells at the opposite end of the sac are called from their position the *antipodal cells* (see Fig. 44, 7 and 8, *an*). In this particular case the antipodal cells disappear before fertilisation (Fig. 44, 9). Lastly, the two free nuclei are called the *polar* nuclei (see Fig. 44, 7, p_1 and p_2, and Fig. 44, 8, *p*), because one comes from each pole of the sac. Their fate is remarkable. They do not remain in their original positions, but travel through the cytoplasm to meet each other (see Fig. 44, 7 and 8). When they meet they fuse together into a single large nucleus, which may be called the secondary nucleus of the embryo-sac (see Fig. 44, 9, *pp*). Meanwhile the whole embryo-sac has increased considerably in size, and so has the egg-apparatus, the two synergidæ becoming long and pointed (see Fig. 44, 9, *s*, *s*).

The body of the ovule during its development becomes considerably curved on itself, owing to the more rapid growth of its lower side, so that the micropyle ultimately comes to point almost backwards

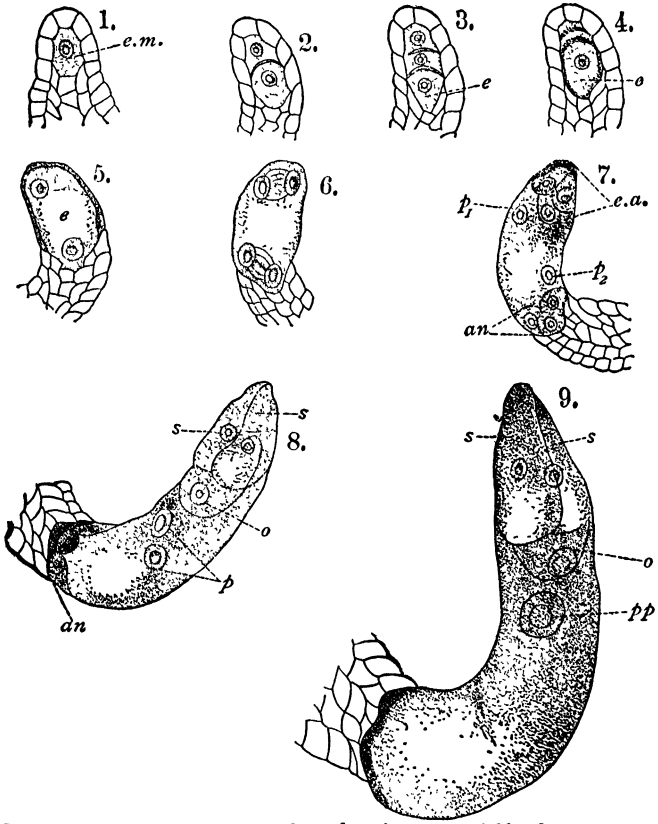


FIG. 44.—Development of ovule and embryo-sac of Shepherd's Purse (*Capsella Bursa-pastoris*). The integuments are not shown. 1, Early stage : *e.m*, archesporium or embryo-sac mother-cell. 2, The mother-cell has divided once. 3, A second division has taken place. 4, The lowest of the three cells, *e* (the embryo-sac), is obliterating the two above it. 5, The nucellus disappears, except at the base ; the nucleus of the embryo-sac has divided. 6, Each daughter-nucleus divides again. 7, Four nuclei at each end of sac ; three at each end have cells around them : *e.a*, egg-apparatus ; p_1, p_2, upper and lower polar nucleus ; *an*, antipodal cells. 8, The polar nuclei approach each other ; *s*, *s*, synergidæ ; *o*, ovum. 9, Fertilisation stage ; *pp*, secondary nucleus, arising from fusion of polar nuclei. Magnified about 200. (After Guignard.)

towards the placenta. The embryo-sac takes part in this curvature (see Fig. 44, 9, and Fig. 43). Ovules in which the nucellus and embryo-sac are bent in this way are called *campylotropous.*

The structure of the ovule, then, when ready for fertilisation, is as follows: it is attached to the placenta by a stalk, the funicle; the curved body of the ovule is enclosed by the two integuments, which leave a narrow opening at the free end, the micropyle; the interior of the ovule is almost entirely occupied by the long curved embryo-sac, which is in immediate contact with the inner integument. The rest of the tissue of the nucellus has disappeared except at the base. Within the embryo-sac, at the micropylar end, are three cells, the egg-apparatus. The most deeply-seated of the three is the ovum. In the cytoplasm of the sac is a large nucleus, which has been formed by the fusion of the two polar nuclei. We shall probably find no trace of the antipodal cells, which at an earlier stage occupied the chalazal end of the sac.

The description just given, though taken specially from the Shepherd's Purse, applies to the ovules of the Wallflower also, except that the latter may have several embryo-sacs side by side. Only one of them, however, contains an ovum capable of being fertilised. Fig. 43 is drawn from an ovule in which only one embryo-sac is visible.

e. Fertilisation

We have next to learn how fertilisation is brought about. The ovum by itself is quite incapable of any

further development. It can only become an embryo or young plant after union with another cell, namely, with one of the generative cells formed from the pollen-grain. The contents of the pollen-grains, therefore, must in some way be conveyed to the ovules in the ovary, in order that fertilisation may take place.

The first stage in this process is that the pollen-grains have to be deposited on the stigma. This is called *pollination*, and is a necessary preliminary to fertilisation. It is easy to prove experimentally that pollination is necessary for the production of ripe seeds, *i.e.* seeds which contain embryos. In order to prove this, the stamens of some of the flowers are cut off before the anthers have dehisced to shed their pollen. It is, of course, essential to do this in good time, and the flower-buds must be opened artificially in order to perform the operation, for as soon as the flower opens naturally the pollen is shed.

The plant must be kept under a bell-glass or under very fine gauze, so that no insects may reach it which might bring pollen from other flowers. There is no danger of pollen being brought by the wind, as the Wallflower pollen is too sticky to be blown about. It is therefore better to use gauze than a bell-glass, as the plant might become unhealthy if kept from the air. It will be found that in all the flowers which have had their stamens removed, and which are not allowed to receive pollen from other wallflowers, the pistils wither away without setting their seeds, and if we examine their shrivelled ovules we find that they contain no embryos. We can prove that it is not the

mere "shock" of the operation which prevents the seeds from ripening, for if pollen from another flower be placed on the stigmas of the mutilated flowers their seeds will ripen in due course, and when they are sown the embryos will grow into young plants as usual.

We learn, then, that the access of pollen to the stigma is a necessary condition for the formation of fertile seeds. It was by experiments of this kind, performed over two hundred years ago, that the existence of distinct sexes in plants was first proved. We thus see that the function of the flower is the sexual reproduction of the plant. We are now in a position to study in detail how the process goes on.

In plants like the Wallflower, which have conspicuous, brightly-coloured, and sweet-smelling flowers, the work of pollination is chiefly performed by insects. The Wallflower is specially attractive to bees, who visit it in search both of honey and of pollen, the "bee-bread," which is collected as food for the young brood. The bees are quite as useful to the Wallflower as the Wallflower is to the bees, for in the course of their visits they do it the essential service of bringing the pollen on to the stigmas of its flowers, and so ensuring fertilisation. We have already seen that there are two large honey-glands or *nectaries* in the flower. The honey formed by these glands collects in the pouches of the inner sepals. As the bee thrusts her proboscis down between the stamens and the pistil in order to reach the honey, her head comes into contact with the inner side of the anthers, on which a mass

of loose pollen is hanging, for the anthers are *introrse*, *i.e.* they open on the inner side. When the bee flies to another flower, it is pretty sure that some of the pollen which has stuck to her head will be brushed on to its stigma. If this happens, as it generally will, *cross-pollination* will be effected, *i.e.* the stigma of one flower will receive the pollen of another, and this will often happen between the flowers of different plants. The chief way in which bees and other insects are of use to flowers is in bringing about cross-fertilisation, which, as Darwin's experiments prove, usually produces more and better seed than fertilisation by pollen of the same flower. In the Wallflower, however, self-pollination is also provided for; the anthers of the longer stamens rise up immediately above the stigma, and some of their pollen will be almost certain to fall upon it. It is also, of course, possible that the insect may happen to brush some of the pollen on to the stigma of the same flower. Probably this does not happen very often; for generally, as the bee works round the flower, one side of its head will touch the anthers, while the opposite side brushes against the stigma. In any case the Wallflower is sure to be cross-fertilised very often; and if this fails, owing to bad weather and the absence of insects, there is still self-fertilisation to be relied on, which is a great deal better for the plant than no fertilisation at all. Many other flowers have much more elaborate arrangements ensuring cross-pollination, and rendering self-pollination impossible, but the simple mechanism of the Wallflower is effective enough. Some flowers, however, as *e.g.* the Garden Pea (***Pisum sativum***), are habitually self-pollinated.

All that an insect directly does for a flower is to perform the act of *pollination*, *i.e.* to bring pollen on to the stigma. If all goes well, this act has its proper effect, *i.e.* the *fertilisation* of the ovules.

Hence it is usual to speak of bees and other insects as *fertilising* flowers, though they are really only concerned in the preliminary process.

Now we will assume that the pollen has reached the stigma, whether by the agency of some insect or directly from the anther, and will see what happens next.

The surface of the stigma, as we have already learnt, is coated with long unicellular hairs or papillæ, between which the pollen-grains are caught. These cells secrete a slightly sticky fluid, containing sugar in solution, which the pollen-grains absorb. In consequence of this they begin to swell, as can be seen under the microscope, and the thin parts of their walls become bulged out. Under the influence of the food which it obtains from the stigmatic fluid, the pollen-grain begins to germinate. At one of the places where its outer coat is thin the protoplasm grows, and forms a protrusion covered by the thin cellulose membrane; this protrusion increases in length and becomes the pollen-tube. The greater part of the contents of the pollen-grain, including all the three nuclei, pass into the tube, which continues its growth, makes its way between the stigmatic cells, and penetrates into the tissue of the style below (cf. Fig. 82, p. 181, from the Lily). It grows on among the cells of the style, and at last reaches the cavity of the ovary. Here the pollen-tube follows the placenta

When it reaches an ovule which is ready for fertilisation, the tube curves away from the placenta, and follows the funicle, until its end reaches the micropyle of the ovule (Fig. 43, *pt*). We are at present unable fully to explain the causes which direct the growth of the pollen-tube with unerring accuracy into the micropyle of the ovule. Recent researches make it probable that the apparent attraction is due to some sugary substance secreted by the ovule. The tube grows on through the narrow passage, and eventually its tip reaches the summit of the embryo-sac, and meets the pointed ends of the synergidæ.

And now the growth of the pollen-tube has reached its limit, and its destination is attained. The length of the tube is enormous compared to the size of the pollen-grain which produced it. In the Wallflower the distance from the stigmatic surface to the lowest ovule in the ovary is about 6 mm. ($\frac{1}{4}$ in.) in a straight line. The diameter of the pollen-grain is about ·02 mm.

The tube does not really grow straight, so that we shall be within the mark in estimating its length on the average at about three hundred times the diameter of the pollen-grain before germination. There are other plants in which the growth is ten times as great, or even more. It is evident that this enormous growth is only possible if food is taken up on the way from the cells of the style and ovary. In fact, the germinating pollen-grain lives at the expense of the tissues of the pistil, just as a parasite lives at the expense of its host. We must not, however, suppose

that the whole tube is filled with protoplasm. The protoplasm with the nuclei is at all stages of growth to be found in the growing end of the tube. All the older part of the tube is almost empty.

It is quite easy to cultivate the pollen-grains and make them germinate, if we provide them with an artificial stigmatic fluid. All that is necessary is to put some of the grains into a drop of sugar-solution on a glass slide, so that we can observe them under

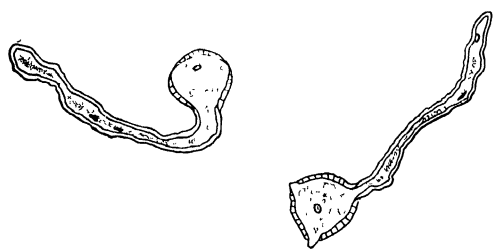


FIG. 45.—Pollen-grains of Wallflower germinating in 6 per cent. sugar solution. Observe the three nuclei, two of which are already in the pollen-tube. Magnified about 200. (R. S.)

the microscope. For the Wallflower pollen a 6 per cent. solution of common sugar (cane-sugar) is about right. In this the grains will put out tubes which reach a considerable length, and the passage of the nuclei down the tubes can be observed. The pollen-tubes figured (Fig. 45) were obtained in this way.

The details of fertilisation have not been followed in the Wallflower, which is not very favourable for the investigation, as the structures in question are small. What follows is a general description based

on observations recorded on other plants. Reference may be made to figures given at pp. 185–187 (Figs. 85, 86, 87), of fertilisation in the Lily, a plant in which all the details have been fully worked out.

All three nuclei travel down the pollen-tube with the protoplasm. The vegetative nucleus, however, *i.e.* that which was the product of the first division (see p. 115), becomes disorganised and disappears, having nothing further to do with the process of fertilisation. The two generative nuclei alone remain, and when the pollen-tube has penetrated the micropyle of the ovule and reached the embryo-sac, these nuclei are to be found in the cytoplasm at the extreme end of the tube. The cellulose wall of the pollen-tube is very soft, and allows the passage of the generative nuclei out of the tube. One of the two generative nuclei passes on, usually between the synergidæ, and reaches the ovum itself. It must be remembered that these cells have no cell-walls, and so no resistance is offered to the passage of the nucleus. Ultimately the generative nucleus reaches the nucleus of the ovum. *The two nuclei then fuse together into one*, and fertilisation is effected. It is probable that in all cases some cytoplasm passes over from the pollen-tube with the nucleus, and unites with the cytoplasm of the ovum. What, however, we at present know to be constant in fertilisation is the union of the *nuclei* of the sexual cells. This statement holds good for plants generally, and not for flowering plants alone.[1]

[1] For the function of the *second* generative nucleus, see below, pp. 134 and 186.

f. Development of the Embryo

The effects of fertilisation are, that the ovum develops into the embryo, the ovule into the seed, and the pistil into the fruit. We will first consider the development of the embryo or young plant, for this is the really important process, to which the changes in the ovule and pistil are subservient.

The immediate result of fertilisation is that the ovum surrounds itself for the first time with a cell-wall. Its nucleus, which, as we have seen, has been formed by the fusion of a generative nucleus from a pollen-grain with the original nucleus of the ovum, next undergoes division. This division of the nucleus is followed by that of the cell, which divides by a transverse wall into two cells. Repeated transverse divisions then go on, until we have a row of several cells (see Fig. 46, A) attached at one end to the wall of the embryo-sac near the micropyle, while the other end of the row hangs freely in the interior of the sac. The last cell at the free end is nearly spherical, and larger than the rest. The whole structure at this stage is called the *pro-embryo.* The round cell at the end is called the *embryonic cell*; the rest of the row is the *suspensor.* From the "embryonic cell" the greater part, but not the whole, of the young plant is formed. This cell first divides by three walls, two longitudinal and one transverse (see Fig. 46, A and B, *e*), cutting each other at right angles, into eight cells, the octants. Next, each octant divides by a wall parallel to the

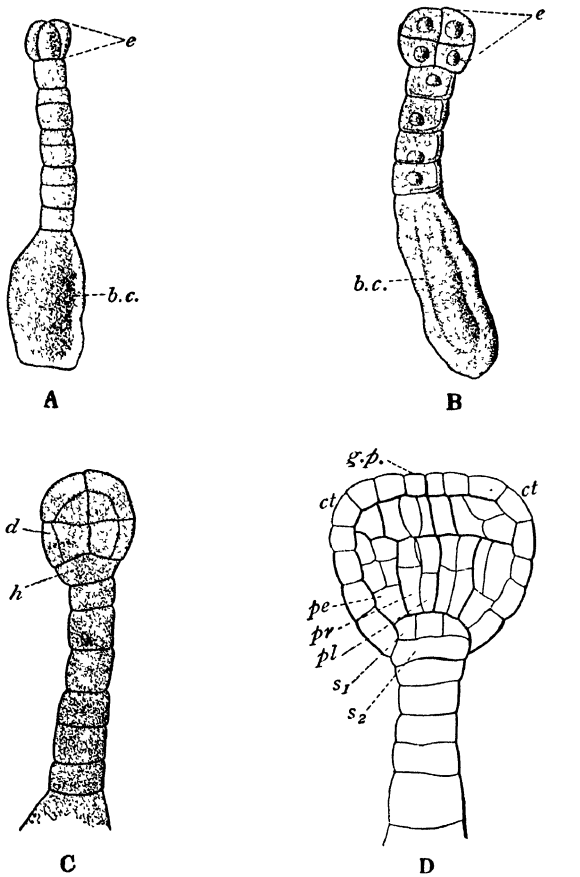


FIG. 46.—Development of the embryo of Shepherd's Purse. *b.c*, basal cell of suspensor; *e*, embryonic group; *d*, dermatogen; *h*, hypophysis; *g.p*, future growing point of stem; *ct*, *ct*, cotyledons; *pe*, periblem; *pr*, *pl*, cells of plerome; s_1, s_2, cells derived from the hypophysis. The micropyle is below the suspensor. (After Hanstein.) Magnified about 200.

outer surface, into an inner and an outer cell. The eight outer cells thus cut off form the dermatogen of the embryo (see Fig. 46, C, *d*). Their further divisions take place entirely by walls at right angles to the surface, so that the layer remains one cell thick. It gives rise to the entire epidermis of the shoot, and to no other tissue. The eight inner cells then divide in their turn, forming a central group and an intermediate layer (see Fig. 46, D). The central group becomes the plerome, from which the central cylinder of the embryonic stem is developed, while the intermediate layer between plerome and dermatogen becomes the periblem, from which the cortical tissues arise.

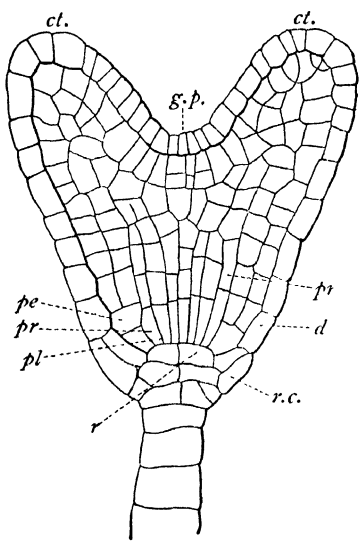


FIG. 47.—Older stage of same; the two cotyledons now project beyond the growing point. *r*, periblem of root; *r.c*, root-cap. Other letters as before. (After Hanstein.) Magnified about 200.

The *hypophysis* or last cell of the suspensor, immediately adjoining the embryonic cell, also contributes something to the formation of the embryo. It divides by a transverse wall, and the daughter-cell next the embryonic cell by its further divisions forms the root-cap and periblem of the root (see Fig. 47, *r.c.* and *r*),

while the plerome of the root is formed from the same central group as that of the stem.

We see, then, that the apex of the root is turned towards the suspensor and the micropyle, as is always the case in the embryos of flowering plants. The apex of the stem is placed exactly at the opposite end of the embryo.

As growth proceeds, the embryo ceases to be spherical. It first becomes flattened at the top and then heart-shaped (see Fig. 47), forming two lateral protrusions. These are the *cotyledons* (Fig. 46, D, and 47, *ct*), the two first leaves of the embryo. The growing point of the stem lies between them (*g.p*), but its development does not begin till later. The class to which the Wallflower belongs derives its name, *Dicotyledons*, from the fact that its embryo normally has two seed-leaves or cotyledons. The growing point of the embryonic stem in this class is constantly terminal (*i.e.* in the middle line of the embryo, at the end farthest from the micropyle), and the two cotyledons lateral (*i.e.* one on each side of the growing point).

As the embryo attains its full size it gradually occupies the whole of the curved embryo-sac, and therefore of necessity becomes curved itself, so that the cotyledons are bent back and lie parallel to the young root or *radicle*. In the Wallflower the cotyledons are so placed that their edges are turned towards the radicle (see Fig. 49); in this case they are said to be *accumbent*. This, however, is a character of no great importance, as it varies in closely-allied plants.

g. The Endosperm

It is now well known that a *double* act of fertilisation takes place within the embryo-sac; in addition to the fertilisation of the ovum, the second generative nucleus from the pollen-tube unites with the secondary nucleus of the embryo-sac, itself, as we have seen, the product of a nuclear fusion. To this subject we shall return when we come to our next type, the Lily (p. 186, Fig. 86). The fertilised nucleus of the embryo-sac undergoes repeated divisions, and around the daughter-nuclei cells are formed. In this way a little tissue is produced, called the *endosperm*, a name given to the tissue thus formed in the interior of the embryo-sac, and outside the embryo, after fertilisation. But in the case of the Wallflower and all its immediate allies, such as the Cabbage, Turnip, Shepherd's Purse, Watercress, and plenty of other well-known plants, the greater part of the endosperm is only a temporary structure. It never attains any considerable size, and is to a great extent used up as food by the growing embryo before the seed is ripe, only the outermost layer being persistent. Seeds which when ripe contain nothing besides the embryo are called *exalbuminous*, because they contain no *albumen*, an old-fashioned name applied to the endosperm and analogous tissues from a fancied

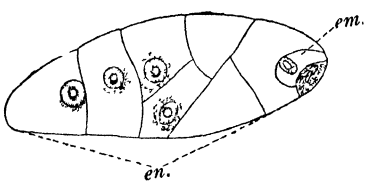


FIG. 48.—Embryo-sac of Elder (*Sambucus*), which has just become filled up with endosperm by cell-division. *en*, endosperm; *em*, embryo. (After Hegelmaier.) Magnified about 250.

resemblance to the white of an egg. The Wallflower seed is commonly described as exalbuminous ; but this is not strictly true, for we know from recent researches that one layer of endosperm at least is persistent. In many plants the embryo-sac becomes completely filled with endosperm, the embryo itself occupying only a small space. Such seeds are said to be *albuminous*. Fig. 48 shows a young embryo-sac filled with endosperm, from the Elder. (See also Fig. 91, p. 191.)

h. The Ripe Seed

We will now complete the description of the *seed*, which is the fertilised ovule, with its contents. The nucellus, as we have seen, disappears in great part even before fertilisation. By the time the seed is ripe scarcely a trace of it remains except a little group of cells at the chalaza, in contact with the tips of the cotyledons of the embryo. The integuments, on the other hand, remain (though some of their layers are obliterated), and develop into the hard seed-coat or *testa*, which when the seed is ripe consists of several layers of cells (see Fig. 49, *t*). On the extreme outside is a layer of clear cells with very thick walls, so thick that there is no cell-cavity left at all. These walls are mucilaginous, and swell up in water, rendering the seed-coat sticky, and causing it to adhere to the soil or to anything which it touches. Beneath this are two or three layers of brown cells, more or less flattened, and on the inside of the seed-coat next the embryo is a layer of thin-walled cells, with very abundant contents, consisting chiefly of nitrogenous food-materials in the form of protein granules

(see p. 38). This innermost layer belongs to the endosperm, of which it is the only remnant. The outermost mucilaginous layer is the epidermis of the outer integument; the brown cells in between belong partly to one integument and partly to the other. The

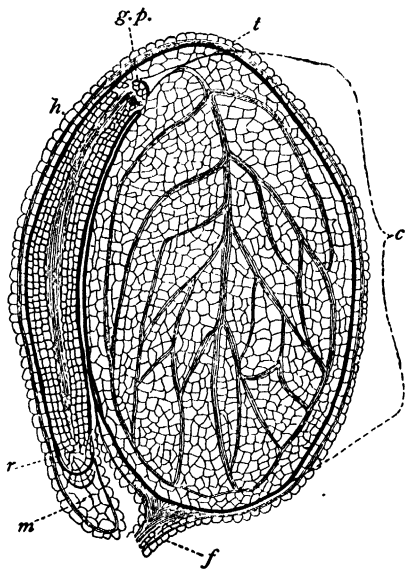


FIG. 49.—Seed of Wallflower in section passing between cotyledons. *h*, *t*, testa; *m*, micropyle; *f*, funicle; *r*, radicle of embryo; above this is the hypocotyl; *g.p*, growing point of stem; *c*, one of the two cotyledons. Magnified about 20. (R. S.)

funicle remains as before, and its vascular bundle can still be traced in the ripe seed. The micropyle is closed while the seed is ripening, but it still has a part to play, as we shall see presently. The ripe seed, then, consists essentially of the funicle, the testa

or modified integuments, and the embryo. The whole interior of the seed is occupied by the large curved embryo. At the end next the micropyle is the *radicle* of the embryo, and above this is the *hypocotyl*. At the upper end of the latter the two broad *cotyledons* are borne, and between them is the *plumule*, or growing point of the stem (see Fig. 49). Many seeds contain a much larger amount of permanent food tissue, in the form of endosperm within the embryo-sac, to be used during germination, *e.g.* Buttercup, Fox-glove, Castor-oil seed; while in a few the nucellus is persistent, forming the *perisperm*, *e.g.* Pepper, Water-Lily.

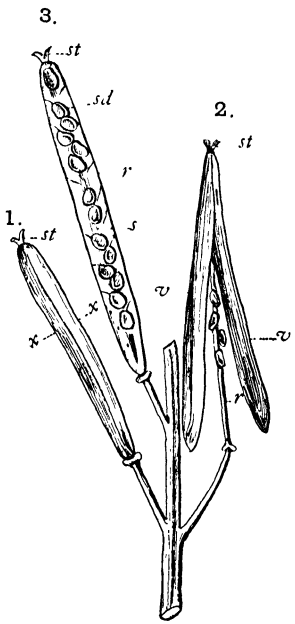


FIG. 49*.—Three mature fruits of the Wallflower, borne on the peduncle.
1. Fruit still closed. *x*, *x*, line of transverse section, as shown in Fig. 50.
2. Fruit dehiscing. *v*, *v*, the open valves; *r*, replum, seen edgeways, with seeds attached.
3. Fruit after valves have dropped off, seen in plane of replum, *r*. *s*, septum stretched across replum; *sd*, seeds, showing parietal placentation; *st*, stigma, in all three fruits.
⅔ of natural size. (R. S.)

i. The Fruit

The pistil ripens into the fruit or seed-vessel. In doing so it increases greatly in bulk, growing from a quarter of an inch to two inches or more in length (Fig. 49*, 1). Its tissues show changes of some interest. Perhaps the most important change

is the development of a layer of very thick-walled, elongated cells (*sclerenchyma*) from the inner parenchyma, adjoining the epidermis which lines the cavity of the fruit. The parenchyma lying between the sclerenchymatous zone and the outer epidermis contains chlorophyll. The outer epidermis is densely clothed with overlapping hairs of the usual Wallflower type, and has numerous stomata.

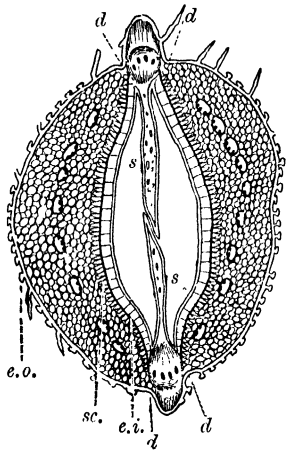


FIG. 50.—Transverse section of young fruit of Wallflower (seeds omitted). *d*, *d*, thin portions of ovary wall, where dehiscence takes place; *s*, *s*, septum, which is in two parts; *e.o.*, outer; *e.i.* inner epidermis; *sc*, sclerenchyma. The thick masses of tissue at the two ends of the septum belong to the replum. Magnified about 8 (R. S.) (Cf. Fig. 49*, and Figs. 9, 10, 11, pp. 19–21.)

As the fruit matures, its tissues give up their water and become dry and rigid. When quite ripe, it splits open, or *dehisces*, owing to the unequal contraction of the harder and softer layers of the carpellary walls. The sides of the fruit split away from the *replum* or persistent placenta, the severance beginning below and extending upwards. The valves thus formed remain for a time attached at the top (Fig. 49*, 2). When they fall the replum is left intact, with the seeds

attached to it, and the papery septum stretched across it (Fig. 49*, 3).

The lines along which dehiscence is to take place are marked out beforehand as thinner bands in the wall (see transverse section, Fig. 50, *d*, *d*). A special layer of separation is formed at these places, the cells of which split apart during dehiscence, and so release the valves.

The seeds hang on to the replum for a time and then fall, or are blown off by the wind, on to the ground.

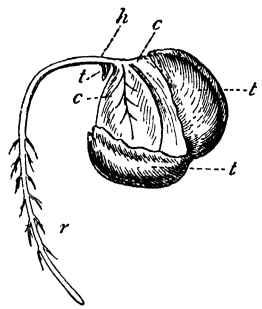


FIG. 51.—Germinating seed of Wallflower. *t*, *t*, burst testa ; *c*, *c*, cotyledons ; *h*, hypocotyl ; *r*, root. Magnified about 5. (R. S.)

k. Germination

When the temperature is sufficiently high, and the weather is moist enough for the seeds to take up a supply of water, the process of *germination* begins.[1] By germination is meant the development of the seedling from the embryo contained in the seed.

The mucilaginous layer of the testa takes up water in large quantities, swells into a slimy coating, and thus helps to fix the seed to the soil. Part of the water which is thus taken up is passed on to the em-

[1] When many seeds are shed they are not *immediately* capable of germination. In some seeds germination is dependent also upon access of oxygen and ready removal of carbon dioxide from the seed. In other seeds, *e.g.* legumes, the seed coat remains impermeable to water for a considerable time despite soaking. If, however, the seed coat is broken, water can enter and germination proceeds.

bryo inside, and stimulates it after its long rest to renewed growth. The hypocotyl and radicle begin to elongate rapidly, and the apex of the latter is forced out through the micropyle. In whatever position the germinating seed may lie, the radicle as soon as it becomes free curves, so that its tip is directed straight downwards, and at once penetrates the soil (see Fig. 51). As soon as this has happened, the young root immediately begins to develop root-hairs, which take a firm hold of the particles of soil, and serve both for nutrition and for the fixing of the plant during its subsequent growth. Meantime the hypocotyl grows very rapidly, and curves so that the apex of the stem comes to point directly upwards. The cotyledons for a time remain imprisoned in the seed-coats, which are lifted up with them above the level of the ground, but they soon spread themselves out flat, and in doing so strip off the seed-coats.

We see, then, that in germination the root grows vertically downwards and the stem vertically upwards, while the cotyledons take an approximately horizontal position. The apex of the stem (*the plumule*) now begins to develop further and form leaves. The root at the same time puts out the first lateral rootlets, and we may now regard germination as completed; the embryo has become a seedling (see Fig. 30, p. 79).

The food-supply necessary for germination is obtained at first from the organic substances (starch, etc.) stored up in the cotyledons themselves, and in part also from the remaining layer of endosperm, which, as we saw above, is rich in protein granules. The food in most seeds is

stored as solids many of which are insoluble in water. Before this reserve food can be used for growth during the process of germination, it must be rendered soluble by the action of enzymes. Insoluble starch, for instance, is converted into soluble sugar by the action of *diastase*. As soon as the root-hairs have taken hold of the soil, the seedling can begin to supply itself with mineral food, but it is only when the cotyledons have expanded and become green that carbon-assimilation can begin and new organic substances be formed. We see, then, that in this plant the cotyledons have a double function; they serve at first as stores of ready-made food for the seedling, and afterwards they act as assimilating leaves, and can manufacture new food on their own account.

In most of the points described the germination of the Wallflower may be regarded as typical of that of the Dicotyledons generally. For example, the exit of the radicle through the micropyle is very constantly the first stage in germination. The behaviour of the cotyledons, however, differs much in different members of the Class. In some plants, such as the Broad Bean (*Vicia Faba*), the cotyledons never rise above the ground at all, but serve simply as storehouses of food, the first assimilating leaves being those of the plumule. In seeds, again, which when ripe contain abundant endosperm, the first duty of the cotyledons is to absorb the food which the endosperm contains, and they do not emerge from the seed (if they do so at all) until this has been accomplished.

CHAPTER II

TYPE II

THE WHITE LILY (*Lilium candidum*, L.)

IT matters little which of the common kinds of Lily we take for our type. The following description refers in the main to the White Lily, but the general Figs. 52 and 53 are of *Lilium auratum*, and some of the other figures refer to different kinds.

The White Lily grows wild in Southern Europe, Persia, and the Caucasus, and is one of the commonest Lilies cultivated in gardens.

I. *EXTERNAL CHARACTERS*

A. VEGETATIVE ORGANS

In cultivation, Lilies are usually raised from *bulbs*. A bulb is really a large underground bud. It consists of a short conical stem, covered with densely-crowded, spirally-arranged, thick scale-leaves, which completely coat the surface, leaving no internodes between them. The base of the bulb produces fibrous roots. The bulb is that part of the plant which persists at all times, in winter as well as in summer. During the winter the

scale-leaves contain stores of food-material, which were laid by during the previous summer, while the green foliage-leaves were assimilating. When growth begins in spring, the short conical axis of the bulb grows straight upwards into a tall stem, producing the foliage-leaves, and ultimately the flowers.



FIG. 52.—General view of flowering stems of *Lilium auratum*. From a photograph. Much reduced; the plant was about 6 ft. high.

The White Lily is peculiar, inasmuch as it produces two sets of green foliage-leaves. One set appears in autumn, arising at the base of the rudimentary flowering stem of the following year. The other set is borne in summer on the tall flowering stem itself. If we examine a plant of the White Lily in autumn, after the flowering stem of the past summer has died down, we see a group of broad lanceolate green leaves, the bases of which are underground, the stem on which they grow being hidden in the earth. These leaves we will call the *ground-leaves*.

If we dig up the whole plant and look at it closely, we find the following structure: on the outside of the bulb there are a number of broad, thick scales, each of which has a blunt, withered tip. These scales (*b*, Fig. 54) are the persistent bases of the ground-leaves of the year before. They are spirally arranged, and if we



FIG. 53.—Flowers of *Lilium auratum*. From a photograph. Reduced.

remove them one by one, we find opposite the innermost of them the decayed base of last summer's flowering stem (*a*, Fig. 54). After these scales are removed, we come upon bud-scales of another kind; these are thick and fleshy like the former, but differ from them in having pointed and uninjured tips (*c*, Fig. 54). The pointed scales are complete leaves which have

never developed any further; they also are spirally arranged. If we remove these, we next come to the green ground-leaves of the present season (*d*, Fig. 54). Their bases are already somewhat swollen, but not nearly so much so as they become later. Removing

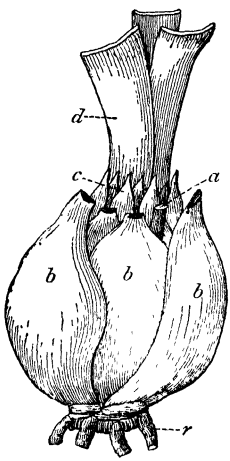


FIG. 54.—Bulb of White Lily in autumn. *r*, roots; *b*, blunt bulb-scales formed from bases of old ground-leaves; *a*, remains of old flowering stem; *c*, pointed bulb-scales of new stem; *d*, ground-leaves of new stem.

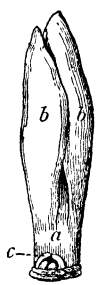


FIG. 55. — Young flowering stem removed from the middle of bulb in Fig. 54. *a*, surface of stem; *b*, undeveloped stem-leaves; *c*, bud from which next year's bulb will arise. (Both after Irmisch.)

these again, we find that they surround a large bud (Fig. 55), which is the young flowering stem ready to develop next summer. The leaves of this bud (*b*, Fig. 55) are simply the future stem-leaves of the

flowering stem. In the axil of the innermost of the *ground-leaves*, and therefore at the base of the young flowering stem, we find a tiny bud (*c*, Fig. 55), with only two or three very minute scales. This is destined to develop into the next year's bulb and stem. We find, then, that the White Lily bulb consists of (1) the base of the old stem, bearing the remains of its ground-leaves, (2) the new stem which arose in the axil of the innermost ground-leaf. On this new stem the first leaves are the pointed bulb-scales which never develop any further; then the ground-leaves, which come up in autumn; and lastly, the stem-leaves, which can only expand when the flowering stem develops next summer. The little bud (*c*, Fig. 55) will repeat this whole process a year hence. In vigorous plants more than one of these buds may be formed, each giving rise eventually to a new bulb.

All Lily bulbs are not so complicated as this. In the Turk's Head (*L. Martagon*), for instance, there are no ground-leaves, and consequently no scales formed from their bases; all the bulb-scales here are of the pointed kind, *i.e.* they are all complete but simplified leaves.

The leaves of the flowering stem are arranged spirally. The phyllotaxis is not very regular, but a divergence of $\frac{3}{8}$ is common, *i.e.* if we trace the spiral upwards, each leaf is in this case separated from the one next above it by $\frac{3}{8}$ of the circumference of the stem.

The leaves are lanceolate in form, without petioles

and have a base which embraces about ⅓ of the circumference of the stem. The autumnal ground-leaves chiefly differ from the stem-leaves in being stalked, and in having a swollen base, and also in their broader ovate-lanceolate form.

The arrangement of the veins in the leaf is different from what we found in our dicotyledonous type. In the Lily all the principal veins run from end to end of the leaf, and are approximately parallel to each other. The veins near the middle of the leaf run almost straight, while those towards the edges are more and more curved, so as to follow the outline of the leaf. There are generally three veins more strongly marked than the rest, the midrib being most prominent of all. These larger veins form projecting ridges on the lower surface. The longitudinal veins are connected by oblique branches. The whole system, therefore, forms a network, but of a simpler form than that in the Wallflower. The longitudinal veins are, on the whole, stouter than the oblique connections. There are, as a rule, no blindly ending branches within the meshes, another point of difference from the dicotyledonous type. The position of the blade of the leaf is roughly horizontal in the stem-leaves, and more oblique in the ground-leaves.

As a rule the flowering stem does not branch; there is a bud in the axil of each leaf, but it generally remains undeveloped. If, however, the main stem be injured, it may be replaced by a branch developed from one of these buds. In some other species, such as *L. bulbiferum*, these axillary buds grow into little

bulbs, which become detached and give rise to new plants, thus affording a good example of *vegetative propagation*. We speak of vegetative propagation when a plant possesses some means of producing descendants without the help of the sexual organs, the stamens and pistil.

In most Lilies such propagation takes place by means of the bulbs. We have already seen that a vigorous old bulb in the White Lily may give rise to several buds, which develop into new bulbs. While the leafy stem is assimilating, the young bulbs receive the food which it forms; part of this they use for their own growth, the rest they store up, especially in the thickened scale-leaves, for future use. Every new bulb can form roots and a leafy stem of its own, and thus ultimately produce flowers, giving rise, in fact, to a complete new plant. In our own country, Lilies are usually propagated from bulbs, seedlings being more rarely met with.

A striking peculiarity of the Lily as distinguished from the Wallflower is the absence of any main root. All the roots of a mature Lily plant are borne on the stem, and are called *adventitious*, as they do not arise from the radicle of the embryo. Usually it is the base of the stem, at the bottom of the bulb, which bears them; sometimes, however, roots also arise from the lower part of the flowering stem above the bulb. When a Lily plant is very young, it has a main root formed from the radicle of the embryo, but this root soon dies away, and the root-system is henceforth entirely produced from the stem. Most members of the Class to which the Lily belongs (*Monocotyledons*) lose their main root early, and replace it by adventitious roots.

B. The Flowers

The flowers are borne in a *terminal raceme, i.e.* they spring from the elongated main axis—the older flowers below, the younger above ; each flower is stalked, and grows in the axil of a small leaf called *a bract.*

The flowers are large, and very easy to examine. The first great difference which we notice, from the Wallflower, is that the whole *perianth,* including both calyx and corolla, is coloured alike, and its leaves are all of about the same size. In the bud, when just about to open, the three outer perianth leaves or sepals enclose all the other organs, only the midribs of the petals showing between them. A good idea of the arrangement of the parts of the flower is obtained by examining a transverse section across a bud (see Fig. 56 ; also diagram, Fig. 78, p. 176).

The *sepals* are three in number, and are all inserted at one level, forming a single whorl. They are lanceolate in shape, and their venation is much like that of the green leaves, only less conspicuous. In the bud each sepal is somewhat hooded, so as to arch over the other organs. At the base of each sepal, on its inner side, is a shallow groove with raised sides, into which honey is secreted.

The three *petals* also form a whorl, and stand opposite the spaces between the sepals, or, in other words, are alternate with them. The petals are narrower at the base than the sepals, but rather broader above. A petal differs from a sepal in having a well-marked midrib, which projects as a ridge on its outer or lower surface. On either side of this ridge

is a deep furrow, into which in the bud the edge of the adjoining sepal fits (see Fig. 56). The side veins of the petal diverge from the midrib, running obliquely upwards and outwards to the edge, these veins being connected by oblique branches to form a network. At the base of each petal is a honey-bearing groove like that on the sepal.

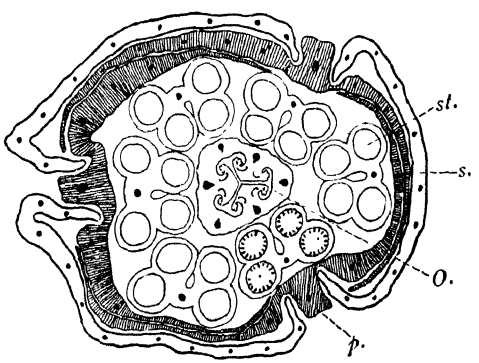


FIG. 56.—Transverse section across a flower-bud of the White Lily. *s*, one of the three sepals (unshaded); *p*, one of the three petals (shaded); *st*, one of the six stamens in two whorls of three; *O*, pistil consisting of three carpels. Magnified about 8. (R.S.) (Cf. Fig. 78, p. 176.)

The *stamens* are six in number, in two whorls of three each. The outer whorl is alternate with the petals, and therefore opposite the sepals. The inner whorl is alternate with the outer, and therefore opposite the petals. In fact, all through the flower the successive whorls of three alternate regularly with each other (see Figs. 56 and 78).

The stamens have long filaments and large *versatile*

anthers, *i.e.* the filament in the mature state is attached to the back of the anther near its middle, so that the anther swings freely upon the filament. In all essentials the structure of the stamen is like that of the Wall-flower, but its large size in the Lily makes it much more favourable for study. The anther consists of a connective and four pollen-sacs. Here, as in our former type, the two pollen-sacs on the same side of the anther become fused when it is ripe, so that the mature anther has only two cavities. Here also the anther is *introrse, i.e.* it opens on its inner side.

In the middle of the flower is the *pistil.* The ovary is cylindrical and ribbed, the style about twice as long as the ovary and surmounted by a large three-lobed stigma (see Fig. 81, p. 179), the velvety surface of which is visible even without a lens. The pistil is syncarpous; the carpels are three [1] in number, and alternate with the inner whorl of stamens. The ovary is three-chambered; the ovules are numerous, and are inserted in two rows in each chamber, arising at its inner angle; in other words, the placentation is *axile* (see Figs. 56 and 78).

If we suppose each of the carpels folded inwards until its edges meet, and then all three carpels closely joined laterally, the united edges of all three meeting at the middle, we shall have a good idea of the structure of the ovary, though not one which is strictly accurate according to the development. In this ovary, as in

[1] On the same view of the morphology of the ovary as that indicated in a footnote on p. 25, E. R. Saunders considers that the ovary of the white lily consists of six carpels, an outer whorl of three which are sterile alternating with an inner whorl of three which are fertile.

many others, the ovules are inserted on that part which corresponds to the margins of the carpels.

The development and minute structure will be dealt with below (p. 173).

II. *INTERNAL STRUCTURE OF THE VEGETATIVE ORGANS*

In the Lily we shall find the same great systems of tissue which we observed in the Wallflower, and their general arrangement is also similar. There are, however, some broad differences between the two types, chiefly connected with the course and development of the vascular bundles.

a. Stem

We shall find it best to begin with the leafy flowering stem (see Fig. 57). If we examine a transverse section through an internode, the first thing that strikes us is the very well defined central cylinder, limited on the outside by a zone of thick-walled cells (*pc* in Fig. 57). In the central cylinder we see the transverse sections of a large number of vascular bundles (*b*). They do not form a single ring, as in our dicotyledonous type, but appear at first sight to be irregularly scattered. We can, however, make out an arrangement in concentric rings, though they are not very regular. Towards the middle of the stem we find the larger vascular bundles forming an irregular ring (b_1). Surrounding these is a zone of smaller bundles (b_2); while quite at the outside of the cylinder, next the thick-walled tissue, we find the smallest bundles (b_3), which

do not, however, form a complete ring. Now, this arrangement in irregular concentric rings is characteristic of the vascular bundles of most Monocotyledons as distinguished from the Dicotyledons, in which we usually find a single and regular ring. This difference in the transverse section depends on the course of the

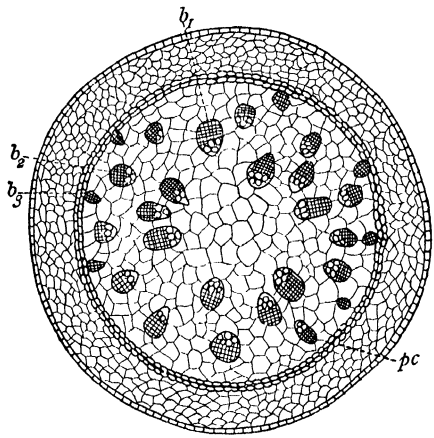


FIG. 57.—Transverse section of the flowering stem of White Lily. Somewhat diagrammatic. *pc*, thick-walled pericycle, forming outer limit of central cylinder; b_3, one of the small vascular bundles on its way from a leaf; b_2, bundle cut through on its inward course; b_1, one of the principal bundles which form the inner ring. Magnified about 20 times. (R. S.)

vascular bundles through the stem. Here, just as in Dicotyledons, all the bundles are *common* to leaf and stem—that is to say, each bundle in the stem is the direct downward continuation of one which comes from a leaf. The diagram (Fig. 58) will help us to understand this, though it is much simpler than the reality.

We see that each bundle on entering the stem from a leaf (*l*) passes very gradually inwards, until it is only a short distance from the middle of the stem. It then turns straight down, and at last joins on to a bundle which starts from a lower leaf. Now, this course is not essentially different from what we found in the Wallflower. The great difference in the transverse section depends on the fact that the bundles pass very gradually inwards, so that when we cut the stem across, our section passes through a number of them at various points of their inward course. Thus the small outer bundles (Fig. 57, b_3) in the transverse section are those which are nearest the leaf and have only just entered the cylinder. (The outline of the cylinder is indicated by dotted lines in the diagram, Fig. 58.) The intermediate bundles (b_2) are cut through at a point nearer the interior; while the largest (b_1) are those which have approached nearest to the centre of the stem and have turned straight down.

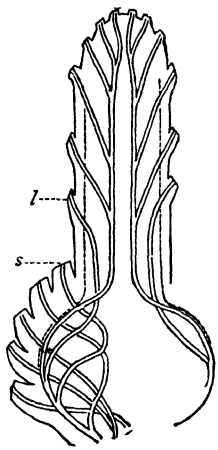


FIG. 58.—Diagram to show course of the bundles in the flowering stem and bulb of the Lilies, as seen in longitudinal section. *l*, insertion of a foliage leaf; *s*, insertion of a bulb-scale. (After Falkenberg.)

In the bulb the course is still more complicated, for here each bundle first bends in towards the middle and then out again, and only joins on to other bundles near the outside of the stem (see lower part of Fig. 58).

In the White Lily three bundles enter the stem from each leaf.

If we now consider the structure of the central cylinder more in detail, we find that the vascular

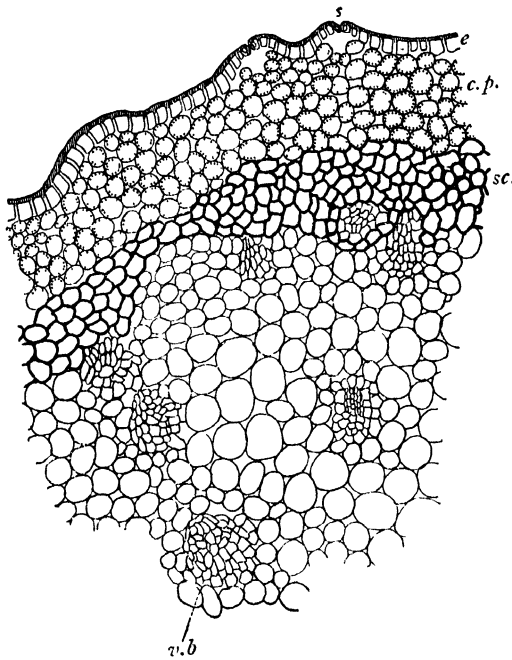


FIG. 59.—Part of transverse section through flowering stem of White Lily. *e*, epidermis; *s*, stoma; *c.p*, cortical parenchyma containing chlorophyll; *sc*, sclerenchyma of pericycle; *v.b*, vascular bundle. Magnified about 70. (R. S.)

bundles are embedded in thin-walled, large-celled ground-tissue (*conjunctive parenchyma*). We may, if we like, call the central part of this tissue within the

innermost ring of bundles *pith*, but there is no distinction in structure between this and the rest of the conjunctive tissue, all the cells of which have the form of vertical cylinders with horizontal ends. They are always living cells, and besides the protoplasm and nucleus generally contain starch granules.

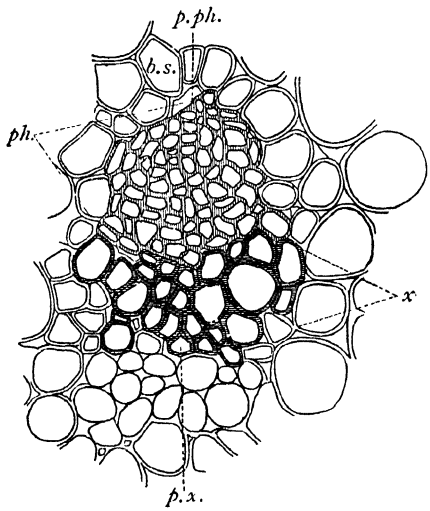


FIG. 60.—Single vascular bundle from the last section. *x*, xylem; *p.x*, protoxylem; *ph*, phloem; *p.ph*, protophloëm; *b.s*, sclerenchymatous bundle-sheath. Magnified 210. (R. S.)

The outer layers (pericycle) of the cylinder, however, are different from the rest. They have thick, lignified walls, and are very long, with pointed ends (*pc* in Fig. 57, *sc* in Fig. 59). As the pericycle forms a rigid case round the cylinder, it is evident that no further growth in thickness is possible. The pericycle

herè represents the chief *mechanical* tissue of the stem, serving to give it the necessary stiffness. The vascular bundles themselves have on the whole a similar structure to those of the dicotyledonous type. They are collateral, the inner half being the wood and the outer half the phloëm (see Figs. 60 and 61). Each bundle

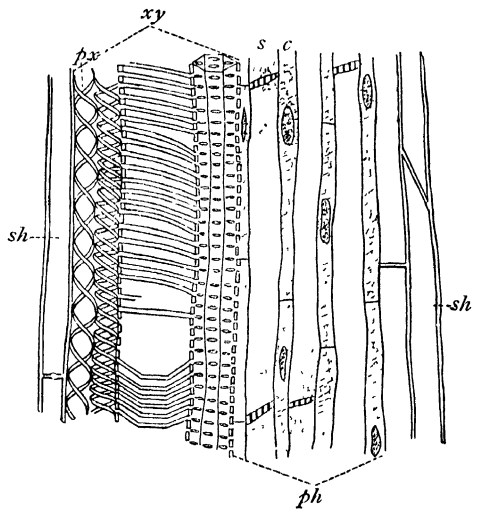


FIG. 61.—Longitudinal radial section through a vascular bundle of the stem of the White Lily. *sh*, bundle-sheath; *xy*, xylem, or wood; *px*, protoxylem; *ph*, phloëm; *s*, sieve-tube; *c*, companion-cell. Magnified 220. (R. S.)

is surrounded by a special sheath of long thick-walled lignified cells (*b.s.* in Fig. 60, *sh* in Fig. 61). There is often a group of thin-walled cells between the sheath and the inner edge of the xylem, which itself consists chiefly of vessels with a few living cells among them. The vessels are of the same kinds as those of

the Wallflower. Starting from the side nearest the middle of the stem, we first find annular or loosely-coiled spiral vessels (often with a double spiral band), then more closely-coiled spiral vessels of larger size, and finally, next the phloëm, vessels with simple pits. We do not usually meet with *bordered* pits in the Lily.

The phloëm is of simple structure, and is entirely made up of sieve-tubes and companion-cells, without any hard bast or phloëm-parenchyma. (Fig. 61, *ph.*) Thus both wood and bast are composed of the same elements as those of the Wallflower, but with rather less variety. There are no mechanical tissues in the vascular bundle.

The *development* of the vascular bundle is also such as we are already familiar with. In the xylem the first elements to be formed are those on the extreme inner edge of the bundle (*px* in Figs. 60 and 61). As usual, this protoxylem may be known by its annular or loosely spiral vessels, adapted to undergo much stretching after their walls are thickened. Conversely, in the phloëm, the first cells to become mature are those on the extreme *outer* edge of the bundle. From these two remote points the development advances towards the middle. But now we come to a great difference from our former type. In the Dicotyledon we found that the development of the young bundle into mature wood and bast was never complete; there was always a band of actively dividing cells left between the two, so that the formation of new wood and bast could go on without limit. In other words, the bundle possessed a cambium, and was therefore said to be *open*.

In the Lily and Monocotyledons generally, on the other

hand, the *whole* of the procambial strand is used up to form permanent tissue. The xylem and phloëm meet; no layer of cambium is left between them; the bundle is a *closed* one, and when once formed is quite incapable of any further growth.

This is one of the most constant distinctions between the two great Classes of which we have taken the Wallflower and the Lily as types. The one has *open* bundles, capable of indefinite growth by means of cambium, while the other (with the rarest exceptions) has *closed* bundles with no cambium, and therefore with limited growth.

Almost all Monocotyledons have closed vascular bundles, and the great majority have no cambium at all, so that the stem or root, when once developed from the growing point, increases no more in thickness. There are, however, a few members of the Class, such as the Dragon-tree and Yucca, which have a kind of cambium, and in which secondary growth in thickness consequently takes place. In these plants the cambium arises altogether outside the vascular bundles, so that the growth is quite different from that in typical Dicotyledons. We need not, however, concern ourselves here with these exceptional cases.

The *cortex* requires little description. Its cells have thin cellulose walls, and in their protoplasm chlorophyll granules are embedded, by means of which the stem is able to do some assimilation. The leaves, however, are the chief organs for this function.

The *epidermis* has elongated cells, and rather numerous large stomata, placed lengthways, so that a transverse section cuts across both guard-cells.

The base of the stem, which bears the scale-leaves of the bulb, has a rather different structure. The distinction between central cylinder and cortex is less sharp; there are no chlorophyll granules in the cortical cells, because this part of the stem is never exposed to light. The vascular bundles have a different course, as explained above. The ground-tissue contains quantities of starch and also oil. The reserve substances of the bulb stem are, however, used up in summer, when the flowering stem develops, and then we find its cells almost empty. The bulb-scales, which we shall describe later on, are more important than the stem as storehouses of food.

b. Leaf

It matters little whether we take an autumnal ground-leaf or a summer leaf from a flowering stem. They are different, as we have seen, in shape, but in internal structure they are very much alike.

We have already learnt the general course of the veins. In the midrib and principal veins of the larger leaves several vascular bundles run side by side; the smaller veins correspond each to a single bundle. If we trace the bundles outward from the stem into the leaf, we find that they immediately begin to branch, the main branches taking a parallel course, while they are connected by minor oblique strands (see Fig. 62, *v.b*).

Thus the whole surface of the lamina is provided with an elaborate system of conducting channels, chiefly differing from that of our dicotyledonous type

in the absence of blindly ending branches, and in the strongly marked parallel course of the stouter bundles. In the broad ground-leaves, however, the parallel veins are less conspicuous, and the network more resembles that of a Dicotyledon.

In these leaves, as in those of most plants, the rule

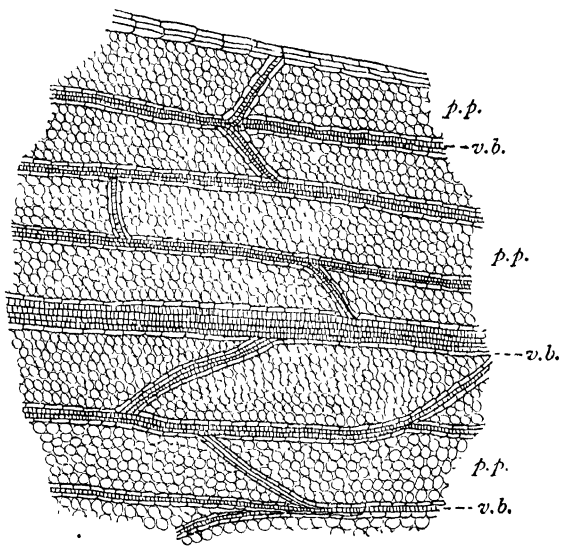


FIG. 62.—Part of section parallel to surface of leaf of Lily. *v.b*, vascular bundles; *p.p*, parenchyma of mesophyll. Magnified about 35. (R.S.)

holds good that the wood of the bundle is directed towards the upper and the bast towards the lower surface.

The minute structure of the bundle in the leaf is like that in the stem. The finer bundles, however, are much reduced, and here we usually find tracheids

instead of vessels (cf. p. 66). The bundles are accompanied by thin-walled parenchyma, and the whole strand, bundle and parenchyma together, is enclosed by a well-marked sheath of cells containing abundant starch (see Fig. 63). The parenchyma accompanying the bundles is continuous with that of the central cylinder of the stem, and it is through this tissue that the sugar formed in the leaf passes down

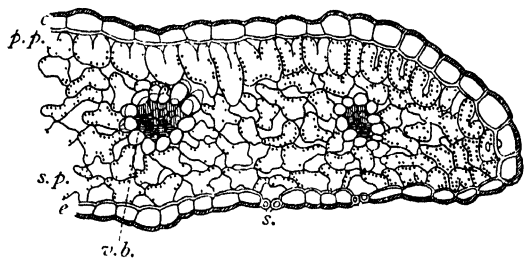


FIG. 63.—Part of transverse section of foliage-leaf of White Lily. *e*, epidermis; *s*, stoma; *p.p* palisade parenchyma; *s.p*, spongy parenchyma; *v b*, vascular bundle, with xylem above and phloem below. Magnified about 70. (R. S.)

towards the bulb, to be there formed into a store of starch.

In this leaf, as in most horizontal leaves, we find that there is a marked difference between the upper and lower parts of the ground-tissue; in fact, we have here, as in the Wallflower, to distinguish between palisade and spongy tissue. The palisade cells, however, are of a peculiar form (see Fig. 63, *p.p*); they are branched, and the branches (two or three to each cell) are placed at right angles to the surface of

the leaf, forming what is called *arm-palisade* tissue. The effect of the branching is that extra vertical wall-surface is gained for the disposal of chlorophyll granules. We must not suppose that this kind of tissue is peculiar to Monocotyledons.

The lower part of the tissue of the leaf is spongy, its cells are branched irregularly in all directions (see Fig. 63, *s.p.*), so as to leave large intercellular spaces between them.

The *epidermis* consists, on both surfaces of the leaf, of large elongated cells, with a thick outer wall, limited by a well-marked cuticle. The stomata are mostly on the lower surface, though we may find a few scattered about in the upper epidermis as well. Each stoma consists of two guard-cells, with a pore between them, leading to an air-chamber below. In fact, their structure is precisely the same as in the Wallflower, but in the Lily they are much larger and easier to observe.

The *bulb-scales* also are leaves or bases of leaves, as we have seen. They have, however, quite different functions to perform from the foliage-leaves, and accordingly have quite a different structure. They are not exposed to light, and therefore have no chlorophyll. The epidermis is without stomata. The ground-tissue is very abundant, and is all alike, there being no need for any special palisade or spongy tissue. The cells are crammed with reserved food-material, especially starch, which is gradually consumed as the flowering stem develops. The vascular bundles are much fewer than in the foliage-leaf, and

their xylem is small, for there is no active water-current to be conducted.

To sum up: while the foliage-leaves are adapted to the functions of carbon-assimilation and transpiration, the scale-leaves of the bulb have only the work of storing up the food which has been formed elsewhere.

c. Root

The main root, as we have already seen, only lasts for a short time, though it grows to a considerable length. After the seedling stage is past, the plant has adventitious roots only. Indeed, as seedling Lilies are not common in our gardens, the only roots which we generally see on these plants are adventitious ones. They usually arise from near the base of the stem, below the bulb-scales (see Fig. 54, *r*). They are somewhat sparingly branched. The roots are of large size, and very favourable for investigation. The general structure follows the same lines as that of dicotyledonous roots, but there is this difference: a root of the Lily, like that of nearly all Monocotyledons, has no secondary growth in thickness, but has to depend entirely on its primary tissues; the latter are accordingly much more highly developed, in the case of the large adventitious roots, than is necessary in a dicotyledonous root, where there is a cambium ready to make good the deficiencies of the original structure.

An adventitious root of a Lily is traversed by a large central cylinder, which includes a great many distinct bundles of wood and bast, often as many as a dozen of each (see Fig. 64). They are arranged alternately all

round the cylinder. We thus see at once that the structure is essentially the same as in the young root of a Wallflower, but in the Lily there are many bundles of wood and bast, while in the Wallflower there were only two of each. In other words, the

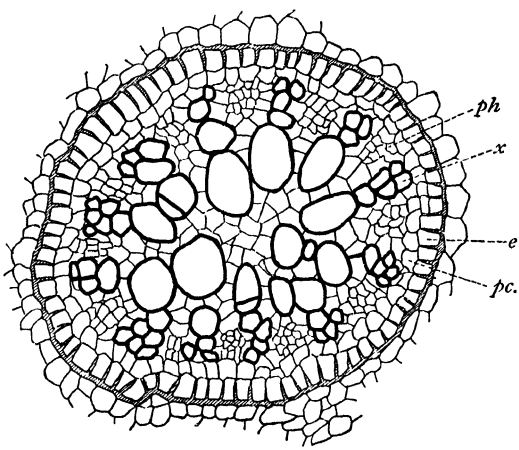


FIG. 64.—Transverse section across the central cylinder, and inner layers of cortex of an adventitious root of the White Lily. *e*, endodermis ; *pc*, pericycle ; *ph*, a phloem group ; *x*, a xylem group ; *protoxylem* at the outer end of each xylem group. Magnified about 150 (R. S.)

root of the Lily is *polyarch*, that of the Wallflower *diarch* (cf. Fig. 28, p. 73). The main root of the Lily seedling, however, which is little more than an embryonic organ, is diarch, like that of the Wallflower.

We notice that here also the smallest vessels lie to the outside of each group of xylem. These are the spiral vessels, which were the first to be formed, so that here, as indeed in all roots, we have *external protoxylem*. The inner larger vessels, which

are formed later, are pitted. Sometimes two of the xylem bundles converge inwards, and meet in a single vessel. The small phloëm groups have the same structure as those in the stem. Xylem and phloëm are separated from each other by a layer of thin-walled tissue. In the root figured there is also some parenchyma in the middle of the cylinder, forming a small pith, but sometimes the xylem groups meet in the middle, so as to leave no room for a pith.

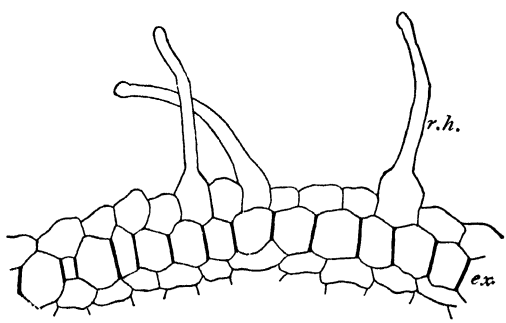


FIG. 65.—Transverse section of tissues at the *extreme outside* of the same root. *r.h*, root-hair; *ex*, exodermis, forming outermost layer of cortex. Magnified 330. (R. S.)

The outermost layer of the cylinder, surrounding the whole ring of wood and bast, is a very definite thin-walled pericycle (Fig. 64, *pc*). Outside this, again, we come to the innermost layer of the cortex, the very conspicuous endodermis (*e* in Fig. 64), the cells of which fit closely together, and have those walls cuticularised by which they are in contact with each other. In the older roots the endodermal cell-walls become thickened, especially on the radial

and external surfaces, as shown in Fig. 64. The endodermis serves especially to cut off all communication between the intercellular spaces of the cortex and the interior of the central cylinder. These spaces contain air, and if this air could make its way into the vessels of the wood, the water-current through the latter would soon be stopped Hence the importance of the isolating endodermis.

The *cortex* is many layers of cells in thickness, and is persistent instead of being thrown off, as in Dicotyledons. Outside this, again, is the absorptive or *piliferous* layer, which forms the external surface of the root. Many of its cells grow out into unicellular root-hairs (see Fig. 65, *r.h.*), which are the special organs for absorption, taking up water and dissolved salts from the soil.

It is only, however, the young parts of the roots which absorb food; sooner or later the piliferous layer dies away, absorption ceases, and the root henceforth becomes merely an organ of conduction, which serves to pass on the water towards the stem. This conducting part of the root requires some kind of protective layer on the outside to guard it against abrasion, or the more serious danger of attack by parasites, and also to prevent possible loss of water if the soil should become dry. The protective function is performed by the outermost layer of the cortex, which soon becomes distinguished from all the inner layers by its cuticularised walls. For a time it has the structure of an endodermis; subsequently the corky change extends to all its walls

alike. Thus the older part of the root is clothed by a complete protective covering, similar to the epidermis of the stem, while the piliferous layer, which formed the original outer surface, disappears. This protective covering, which is called the *exodermis* (*ex* in Fig. 65), is found in many dicotyledonous roots also, but in them its functions are very temporary, and it is usually soon replaced by secondary periderm. In most monocotyledonous roots there is no periderm, and here the exodermis continues to be the only protective layer throughout the life of the root.

The tip of the root is enclosed in a root-cap, the development of which will be described below.

d. Growing-Points and Mode of Branching

The growth of the stem follows the same general course as that of a Dicotyledon. Here also the growing-point, where new tissues and organs are produced, lies at the apex of the stem. In this position we find a meristem, which at first is made up of quite uniform cells. The description given of the growing-point of a Dicotyledon holds good here with only slight differences (see Fig. 66). The ex-

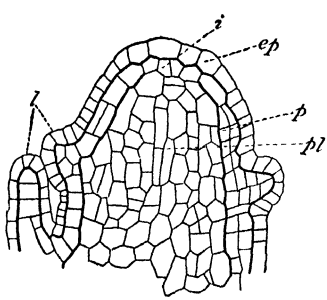


FIG. 66.—Longitudinal median sections of the growing point of the stem in a Monocotyledon. *ep*, epidermis; *p*, periblem; *pl*, plerome; *i*, initial cells common to periblem and plerome; *l*, young leaves. Magnified about 200. (After Douliot.)

ternal layer of the apex is the dermatogen, from which the epidermis is formed. The periblem and plerome probably have a common initial group. From the plerome, which is the inner part of the meristem, the vascular cylinder, including all its bundles, is developed. The development of the vascular bundles begins at the interior of the cylinder and advances outwards. When the outermost bundles have been formed, the pericycle thickens its cell-walls, and all further development ceases.

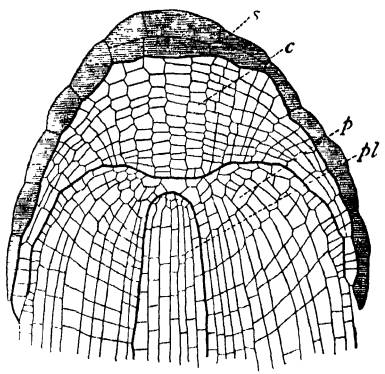


FIG. 67.—Longitudinal median section of apex of young root of a Monocotyledon (*Amaryllis*). *s* (shaded), "digestive sac," formed from endodermis of parent-root; *c*, calyptrogen, giving rise to root-cap only; *p*, periblem (the outermost layer formed from this bears the root-hairs); *pl*, plerome. Magnified about 150. (After Van Tieghem and Douliot.)

The leaves here, as usual, develop from below upwards, so that the youngest are always nearest the apex. It is mainly the outer layers of the growing-point which take part in the formation of the leaves and branches of the stem (see Fig. 66, *l*). The growth of each leaf after its first origin goes on chiefly at its base.

The apex of the root is on the whole similar to that of a Dicotyledon, and we find the same three layers of meristem, giving rise to the root-cap, cortex, and vascular cylinder respectively. The superficial

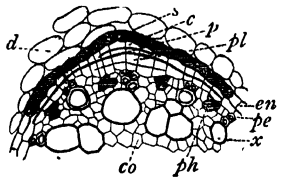


FIG. 68.—Part of transverse section of root of a Liliaceous plant, showing the first origin of a rootlet. *d*, cortical cells; *en*, endodermis; *pe*, pericycle; *x*, xylem group; *ph*, phloem group; *co*, conjunctive tissue. All the above belong to the parent-root. *s* (shaded), digestive sac, formed from endodermis; *c*, calyptrogen, or cells giving rise to the root-cap of the rootlet; *p*, periblem, which will form its cortex and piliferous layer; *pl*, plerome, from which the central cylinder will be developed.

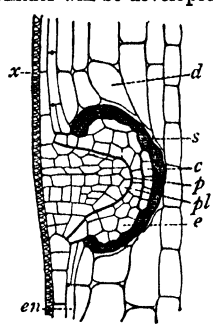


FIG. 70.—Part of longitudinal section of a monocotyledonous root passing through a developing rootlet. Letters as above. (All three Figs. are magnified about 150, and are after Van Tieghem and Douliot.)

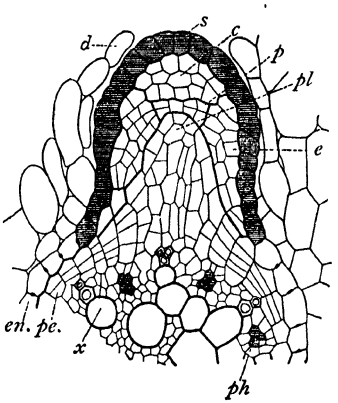


FIG 69.—Similar section from the White Lily, showing a more advanced rootlet. *d*, cortex of parent-root, through which the rootlet is boring its way; *e*, cortex at base of rootlet. Other letters as above.

layer of the root, which bears the root-hairs arises here, however, from the same group as the cortex, instead of having a common origin with the root-cap, as in Dicotyledons (see Fig. 67, and compare it with Fig. 33, p. 86).

The *branching* of the root can also be dismissed in a few words, as in all important respects it takes place in the same way as in the Wallflower.

Here, just as in Dicotyledons, the rootlet arises from a deeply-seated layer of the parent-root, namely, from its pericycle. The details of the development are sufficiently shown by Figs. 68, 69, and 70. The endodermis of the parent-root here takes some part in the process, as it forms a sheath around the developing rootlet during its growth through the cortex. As this endodermal sheath serves to absorb the cortical tissues, through which the rootlet as it were eats its way, it bears the name of the "digestive sac." When this function has been performed, the sac is cast off, the whole permanent part of the rootlet being thus formed from the pericycle.

The origin of an *adventitious* root is similar to that of a rootlet. Just as a rootlet arises endogenously from the parent-root, so does an adventitious root arise endogenously from the stem, and in both cases it is the pericycle from which the new organ is formed.

Summary of Monocotyledonous Anatomy

The general working of the vegetative organs in the Monocotyledons goes on in the same way as in our first type. In both, the green leaves, by means of their palisade and spongy tissue, are the great organs of assimilation and of transpiration. The leaves are in communication with the stem through the vascular bundles and the tissue immediately surrounding them. The conducting tissues divide up their work as follows: the wood serves chiefly to convey the water and mineral salts taken up by the roots; the phloëm

helps to conduct to the growing organs and reserve-stores, the food which has been assimilated in the leaves, and especially that which contains nitrogen. On the other hand, the carbohydrate foods produced by the leaf, such as sugar, are conveyed through the thin-walled parenchyma which accompanies the bundles. Both in Monocotyledons and in Dicotyledons all these tissues are continuous throughout the central cylinder of the stem and its branches, and ultimately with the corresponding tissues of the root. Neither as regards structure nor function can we point to any profound difference between the two Classes, *so far as the primary tissues are concerned.* The real distinction lies in the fact that in typical Monocotyledons there are *no secondary tissues*; the entire structure is developed from the growing points once for all, and henceforth no further additions are ever made, however long the plant may live. Consequently, we generally find that the primary structure of stem and root is more complex in Monocotyledons than in the other Class, because in the former the primary tissues have to do all the work, while in the Dicotyledons they are supplemented, or even entirely superseded, by the secondary tissues formed from the cambium. The few Monocotyledons which have a kind of cambium are here left out of consideration.

This difficulty, however, arises: many Monocotyledons, when mature, have a stem which is of great thickness compared with that of the same plant when a seedling. Take the Maize, for instance: a well-grown plant may have a stem two inches in diameter, while

the stem of the seedling is perhaps an eighth of an inch thick. In the Palms the difference is much more striking; the thin stem of the seedling, only a small fraction of an inch in thickness, may give rise to a great trunk, two feet or more in diameter, and yet there is no cambium and no formation of secondary tissues. How is this possible? The explanation is that the thin stem of the seedling never does become any thicker, but for a time the vigour of the growing point constantly increases, so that each node and internode which is added to the stem is thicker than the last. Thus for a time the stem has the form of a cone standing on its apex. But sooner or later the growing-point reaches its full strength. From this time onwards the portions of the stem which it successively produces are of equal diameter; thus all the upper part of the stem is cylindrical. The first-formed part of the stem, which alone has the shape of an inverted cone, generally becomes buried in the ground, or like the tap-root it may die away altogether. While the whole plant is still very young, the stem and main root have a simple structure, comparable to that of a dicotyledonous seedling at a corresponding stage.

In typical Monocotyledons, then, the increasing diameter of the stem is due to the addition of successively thicker nodes and internodes, and not to the growth in thickness of those already formed.

III. *INTERNAL STRUCTURE AND DEVELOPMENT OF THE REPRODUCTIVE ORGANS*

The flower of a Lily is not only very favourable for study, from the large size and simple arrangement of

all its parts, but it has the more important advantage that it is an excellent type of the flowers of Monocotyledons generally, most of which are built on the same ground-plan. We already know the external characters of the flower; we will now shortly trace its development.

a. Development of the Flower

The flower-bud arises, like any other branch of the stem, from the external layers of tissue of the growing-point, with which it is directly continuous. It is formed in the axil of a bract, and in some species, as in that figured, the axis of the flower itself produces a small lateral vegetative leaf, termed a bracteole (see Fig. 71, B, *b*). In the White Lily, however, the latter is absent. The future flower has at first a broadly rounded shape. The earliest stage shown in the figures is that just after the sepals have appeared. All the three sepals do not arise at the same time, but one after the other (see Figs. 71 and 72, *s*). Next, the three petals appear, all at the same time, and exactly between the sepals (see Fig. 73, *p*). After this, three fresh outgrowths show themselves just inside the petals, and alternating with them, so that they lie exactly opposite the sepals; these are the three outer stamens (st^a, Fig. 74). Very soon afterwards the three inner stamens appear (st^o, Fig. 75) exactly between the first three, and therefore opposite the petals. Lastly, around the centre of the growing point, yet three other structures arise, each shaped like a horseshoe, open towards the inside of the flower. These are the *young carpels*, forming the pistil, which is the innermost whorl of the flower

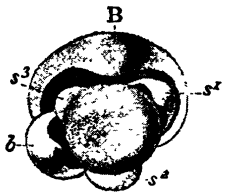


Fig. 71.

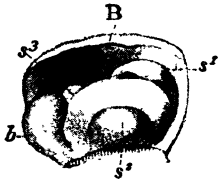


Fig. 72.

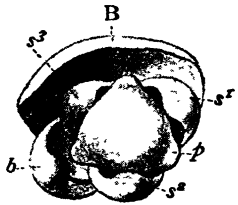


Fig. 73.

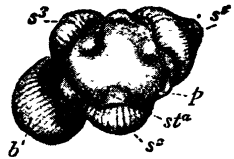


Fig. 74.

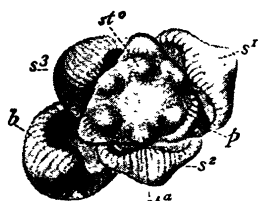


Fig. 75.

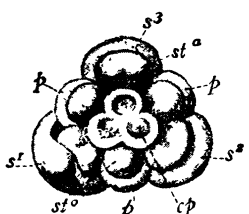


Fig. 76.



Fig. 77.

FIGS. 71 to 77.—Development of flower of a Lily. B, Bract: *b*, bracteole; s^1, s^2, s^3, sepals in order of origin; *p*, petals; st^a, outer whorl of stamens; st^o, inner whorl of stamens; *cp*, carpels. FIG. 71.—Very young flower-bud seen from above; only the sepals have been formed. FIG. 72.—Similar bud seen from the side. FIG. 73.—Older bud, showing the beginning of formation of petals, seen from above. FIG. 74.—Bud in which the three outer stamens have just appeared. FIG. 75.—Bud in which the three inner stamens have also appeared. FIG. 76.—Bud in which all the carpels have appeared. FIG. 77.—Young pistil seen from above while still open: *cp*, carpel; *pl*, placenta. (All the above after Payer.) Magnified.

(Figs. 76 and 77, *cp*). The carpels are alternate with the inner whorl of stamens, and are therefore opposite the outer stamens. During the development of the floral leaves, the stalk, on which the whole flower-bud is borne, goes on growing.

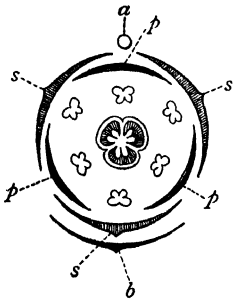


FIG. 78.—Floral diagram of a Lily. *a*, axis of inflorescence; *b*, bract; *s*, sepals; *p*, petals. Within this are seen the two whorls of stamens, and in the middle the three carpels united to form the ovary with axile placentation. (After Eichler.)

We see, then, the extreme regularity and simplicity of the Lily flower. All the whorls consist of three members each, they arise in regular succession, and the members of each whorl always alternate with those of the whorl next outside them. The diagram (Fig. 78), representing a ground-plan of the flower, illustrates this regularity (cf. Fig. 56, p. 150).

b. Structure of the Perianth and Stamens

The calyx and corolla are much alike in their structure, in which they resemble foliage-leaves, but are somewhat simpler. The same systems of tissue, vascular bundles, mesophyll, and epidermis, are present, and the epidermis possesses stomata. The mesophyll, however, is destitute of chlorophyll granules, and in the White Lily has no colouring matter at all. In the yellow Lilies, such as the Tiger Lily, chloroplastids are present, and where we get a distinctly red tint, as

in the spots on *Lilium auratum*, this is due to the presence of red cell-sap.

The groove at the base of each sepal or petal is lined by a tissue of thin-walled cells, rich in protoplasm, by which the nectar or honey is secreted.

The stamens require no detailed description, as they have essentially the same structure as those of

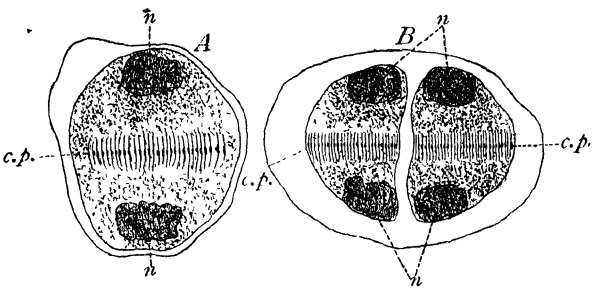


FIG. 79.—Division of the pollen mother-cell in a Lily. *A*, First division: *n*, *n*, daughter-nuclei; *c.p*, granular cell-plate, from which the new cell-wall will be formed. *B*, Second division: *n*, *n*, the four granddaughter-nuclei; *c.p*, *c.p*, the cell-plates from which the second cell-walls will be formed. The four cells in *B* become the pollen-grains. (After Strasburger.) Magnified 800.

the Wallflower, though they are much larger. The development, both of the stamen as a whole, and of the anther with its four pollen-sacs, takes place in the same way as in Dicotyledons.

In each of the pollen-sacs there is a layer of tissue (*archesporium*), which gives rise to a great mass of pollen mother-cells. The division of a pollen mother-cell to form its four pollen-grains, which takes place

in a slightly different way from that usual in Dicotyledons, is shown in Fig. 79.[1]

In the pollen-grain itself further changes take place. The nucleus divides, and around one of the two nuclei thus produced a small cell is formed (see Fig. 80, *g*).

This, as in the Wallflower, is the *generative* cell, so called because it is directly concerned in fertilisation. It is much more easily seen in the large pollen-grain of a Lily than in the small one of a Wallflower. The membrane of the ripe pollen-grain is cuticularised, and its surface is rough with raised ridges, which form a delicate network. Along one side of the grain there is a fold, the membrane of which is thicker than the rest of the wall; it is smooth, and consists of pure cellulose. In the contents of the grain there are many starch granules.

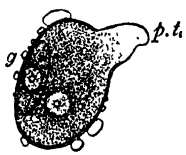


FIG. 80.—Pollen-grain of Lily at the beginning of germination. *g*, small generative cell with its nucleus; *p.t*, first outgrowth of pollen-tube. Oil drops are shown outside the grain. Magnified several hundred times. (After Dodel-Port.)

The dehiscence of the anther takes place as described in the Wallflower. Here also the wall separating the two pollen-sacs on the same side of the anther breaks down at the moment of dehiscence (see Fig. 40, of Wallflower, p. 111), so that the perfectly ripe anther appears to have only two compartments instead of four. The abundant pollen is set free, but most of

[1] For the whole development of the stamen careful reference must be made to the description given in the case of the Wallflower (pp. 109–114).

it remains hanging on the burst anthers, for the grains are made sticky by the presence among them of innumerable drops of oil, of an orange colour.

c. Structure of the Pistil

The pistil has a very different structure from that of the Wallflower, though it resembles that of many other Dicotyledons, so that the differences in question are not characteristic of the two Classes. We have already seen that each of the three carpels arises as a ridge, shaped like a horseshoe, on the growing point of the flower; very soon the ridge is completed on the inner side of each carpel, which thus becomes a closed ring. Where the carpels join on to each other they are completely united from the first, the wall separating their cavities being a single, and not a double one; the pistil is, in fact, completely *syncarpous*. Henceforward growth goes on at the base of the pistil, and so the whole structure grows up into a triple tube. At last the upper edges of each carpel join together at the top, so as to close the tubes. The upper closed part of the pistil develops into the style. At the extreme tip the three carpels remain partly distinct, forming the three lobes of the stigma (see Fig. 81, *stig*), which here correspond in position to the

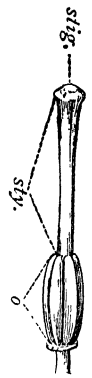


Fig. 81.—Young pistil of a Lily. *o*, ovary; *sty*, style; *stig*, stigma. Natural size. (After Dodel-Port.)

carpels, unlike the arrangement which we found in the Wallflower (see p. 106).

The ovules develop from the inner angle of each of the united carpels, forming two rows in each carpel (see diagram, Fig. 78). This *placentation* is known as *axile*.

d. Ovules

Passing on now to the ovules themselves, we find that the first stages of their growth are like those of the Wallflower, and here also the ovule soon becomes curved. The curvature, however, takes place in a different manner. In the Lily the nucellus and integuments remain straight; the bending takes place at the chalaza, so that the whole body of the ovule turns through an angle of 180°, and so comes to lie parallel to the funicle, with the micropyle directed towards the placenta, which it closely approaches (see Fig. 83). Such an ovule is called *anatropous*. The difference between this form and the *campylotropous* ovule of the Wallflower, in which the nucellus and integuments are themselves bent, will be evident on comparing Fig. 83 with Fig. 43, p. 117. The anatropous ovule is the commonest form both among Dicotyledons and Monocotyledons.

In the Lily the second or outer integument does not become closed, but remains widely open, the narrow micropyle being thus formed by the inner integument alone (see Fig. 83). This is common among Monocotyledons. In other respects there is a general agreement between our two types; in fact,

the main points in the development of the ovule are very uniform throughout the great majority of the members of both classes.

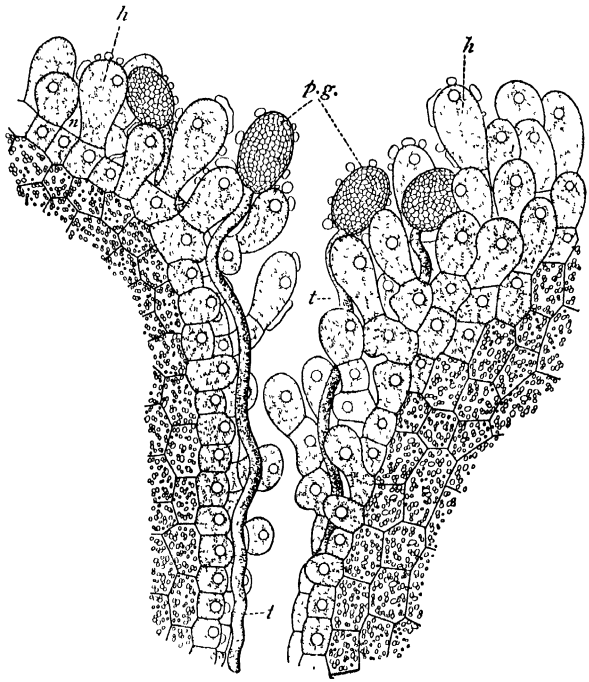


FIG. 82.—Longitudinal section through part of the stigma of a Lily, showing germinating pollen-grains. *h*, papillæ of stigma ; *p.g*, pollen-grains ; *t*, pollen-tubes. Highly magnified. (After Dodel-Port.)

When we come to the origin of the embryo-sac itself, however, there are some differences to note, though they are not characteristic of the two Classes, as similar variations are found within the limits of

both Monocotyledons and Dicotyledons. In the Wallflower we found that the original archesporial cell underwent several divisions before the embryo-sac was finally marked off. In the Lily the matter is simpler: a cell of the middle row of the nucellus, next under its epidermis, grows larger than the rest, and itself becomes the embryo-sac, usually without any further divisions. It grows to a comparatively large size, so much so that there are no plants more favourable for the study of the embryo-sac than the Lilies. The divisions of the nucleus follow the same general course as that described above (see p. 119). We find as the final result three nuclei at the end of the sac towards the micropyle, three at the opposite end and two near the middle. The three nuclei next the micropyle have cells round them, though without any cell-wall; these three cells are the *egg-apparatus*, the *ovum* being the deepest seated of the three, while the two others are the helpers or synergidæ (see Fig. 84, *s*). In like manner the three nuclei at the other end become the centres of the antipodal cells, which, unlike their opposite neighbours, have cell-walls. The two polar nuclei are of exceptionally large size, especially the one from the antipodal end (see Fig. 84, p_2). A more interesting fact is, that these two nuclei do not fuse till very late — in fact, not till after fertilisation. On the whole, however, the processes inside the embryo-sac are closely similar to those in the dicotyledonous type, the description of which should be carefully compared (pp. 119–122).

The nucellus of the Lily does not disappear, but encloses the embryo-sac until after fertilisation (see Fig. 83).

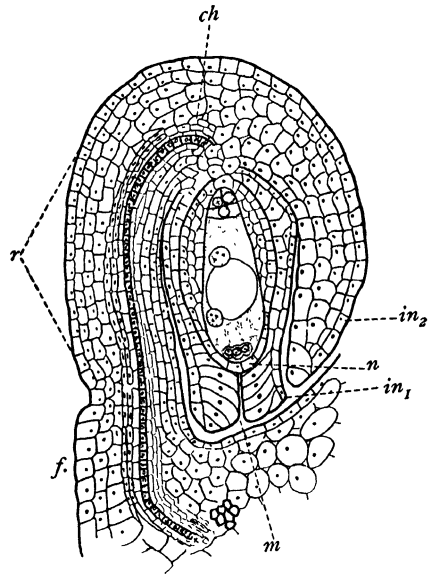


FIG. 83.—Longitudinal section of ovule of Lily. *f*, funicle; *r*, raphe; *ch*, chalaza; in_1, inner integument; in_2, outer integument; *m*, micropyle; *n*, nucellus. Within the nucellus (*n*) is seen the long pear-shaped embryo-sac containing egg-apparatus, polar nuclei with vacuole between them, and antipodal cells. Magnified 82 diameters. (R. S.)

e. Pollination and Fertilisation

The pollination of Lilies is carried on by moths and butterflies, which come in search of the honey secreted by the nectaries on the perianth. The flowers are made

very conspicuous to the visitors by their great size and bright colours, and in some species the sweet smell is an additional attraction. Generally the style projects so far that an insect comes into contact with the stigma before touching the stamens. Hence it will usually bring pollen from the flower which it has last visited, and will thus effect cross-pollination. But it may sometimes happen that the anthers and stigmas of the same flower brush against each other, and that self-pollination may result. As the visits of the insects are rather uncertain and very dependent on weather, this possibility of fertilisation by its own pollen may be of use to the Lily as an extra chance of setting its seeds.

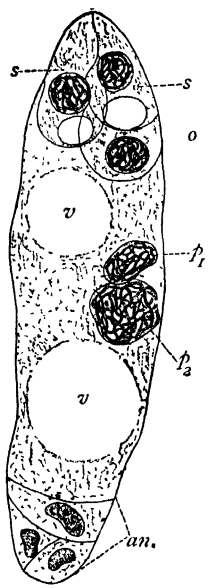


FIG. 84.—Embryo-sac of a Lily. *s*, *s*, synergidæ; *o*, ovum; *v*, *v*, vacuoles; p_1 and p_2, the polar nuclei; *an*, antipodal cells. Magnified about 250 diameters. (After Guignard.)
Note that this figure is reversed as compared with Fig. 83.

When the pollen-grains, by one means or the other, are brought into contact with the stigma, they stick to its viscid surface and soon begin to send out their tubes. The grain takes up water from the stigma, and begins to swell. The fold of pure cellulose (see p. 178) bulges out, and, following the growth of the cytoplasm within, forms the membrane of the pollen-tube (see Fig. 80).

The tube at first creeps along among the papillæ of the stigma, and then grows down between the lobes and penetrates the middle of the style, until its growing end reaches the ovary (see Fig. 82). Here it grows along the surface of the placenta, and at last turns aside into the micropyle of an ovule. Its growth still continues, until it makes its way between the cells of the nucellus to the embryo-sac, which it enters, usually penetrating for a short distance between the synergidæ to the ovum (see Fig. 86). Here the growth of the tube ceases. The length which it has attained is enormous compared to the size of the pollen-grain, for in a large Lily the nearest ovule may be as much as six inches from the surface of the stigma.

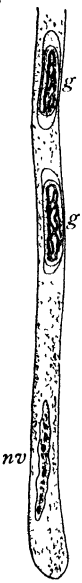


FIG. 85.—Pollen-tube of a Lily on its way down the style. *g*, *g*, the two generative cells, each nearly filled by its large nucleus; *nv*, vegetative nucleus, already becoming disorganised. Magnified about 450 diameters. (After Guignard.)

The large size of the pollen grains and tubes has rendered it possible to trace exactly what is going on inside, and these changes have been followed more minutely in the Lilies than in any other plants. When the pollen begins to germinate, the vegetative nucleus belonging to the large cell of the pollen-grain is the first to enter the tube. It takes the lead all through so long as it exists, but it becomes gradually disorganised, and before the ovule

is reached is altogether lost in the cytoplasm. The small generative cell follows the vegetative nucleus into the tube and immediately divides, so that there are now two such cells, one behind the other, each with a large elongated nucleus (see Fig. 85). When the embryo-sac is reached, the nuclei of both generative cells, accompanied by part of their cytoplasm, pass out through the yielding membrane at the end of the tube, assuming a curved, vermiform shape. One of the male nuclei, probably by its own active movements, enters the ovum, and reaches its nucleus. The two nuclei—male and female—then apply themselves closely together, and probably some of the cytoplasm from the generative cell also unites with that of the ovum. Fertilisation is now accomplished (Fig. 86, *g.n.*[1], *o.n.*), and the ovum next acquires a cell-wall of its own.

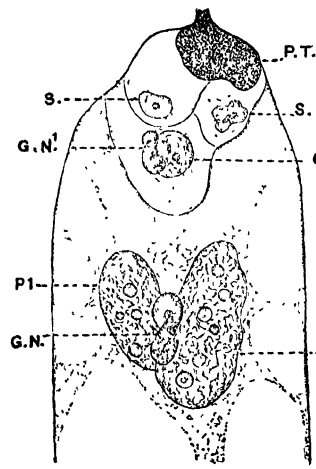


FIG. 86.—Upper part of embryo-sac of a Lily, showing double fertilisation. *p.t.*, end of pollen-tube; *s*, *s*, the two synergidæ; *g.n.*[1], one of the vermiform generative nuclei from the pollen-tube in contact with the nucleus of the ovum, *o.n.*; *g.n.*, the other generative nucleus from the pollen-tube, in contact with the two polar nuclei, p^1 and p^2. Magnified about 400. (After Guignard.)

In the meantime, as modern researches have shown, a second act of fertilisation has taken place within the embryo-sac. The other generative nucleus passes down through the cytoplasm of the sac; it increases in size, and its long, worm-like form is very characteristic, suggesting a power of wriggling motion. It then attaches

itself to the two polar nuclei, which have approached each other, but not yet fused (Fig. 86, *g.n.*, p_1, p_2). Ultimately all three nuclei unite into one, so that the secondary nucleus of the embryo-sac is the product of a triple fusion, one of the component nuclei belonging to the male, and two to the female parent. It is to this triple union that the endosperm owes its origin.

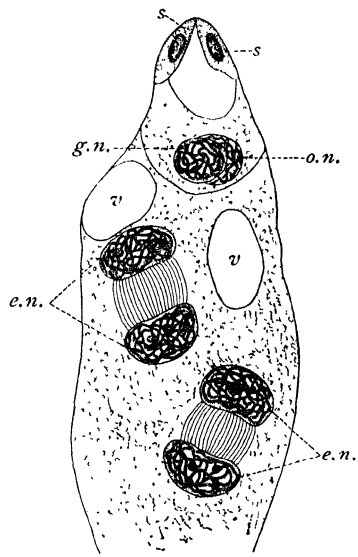


FIG. 87.—Part of the embryo-sac of a Lily, just after fertilisation. *s*, *s*, remains of the synergidæ; *g.n*, generative nucleus, *o.n*, nucleus of ovum (these are now closely united); *v.v*, vacuoles, *e.n*, *e.n*, endosperm nuclei in course of division. Magnified about 250 diameters. (After Guignard.)

Thus fertilisation in Angiosperms is double, the one act giving rise to the embryo, the other to the endosperm.

The synergidæ, having done their work, which probably consists in guiding the end of the pollen-tube to the ovum, now disappear. The antipodal cells also undergo no further development. The embryo-sac is in future shared between the embryo and the endosperm, which latter structure is much more important here than in the Wallflower.

f. Development of the Embryo

We need only describe fully those points in the formation of the embryo in which the monocoty-

ledonous and dicotyledonous Classes differ. These differences are important, and among them we shall find one of the most constant points of distinction between the two divisions.

The nucleus of the fertilised ovum, consisting of the united male and female nuclei, divides, and this is followed by the division of the ovum as a whole. The first two walls formed are transverse. Of the three cells thus produced, the one next the micropyle (which we will speak of as *the lowest*) undergoes no further divisions, but often grows to a great size, as in the embryos shown in Figs. 89 and 90, and then forms a temporary store of food for the embryo.

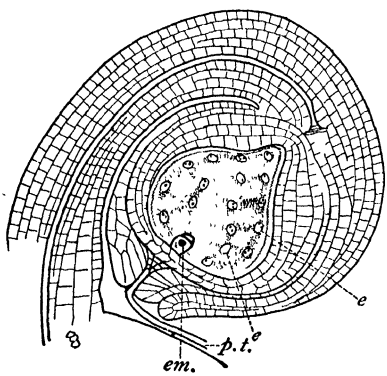


FIG. 88—Longitudinal section of ovule of *Scilla* (a plant allied to the Lily) after fertilisation. *p.t*, pollen-tube; *em*, embryo; *e*, *e*, endosperm nuclei still free in the protoplasm of the embryo-sac. Other parts as in Fig. 83. Mag. 55 diameters. Somewhat diagrammatic. (R. S.)

The *uppermost* cell, instead of forming nearly the whole of the embryo, as in our dicotyledonous type, here only gives rise to one part, namely, the single seed-leaf or cotyledon, which in this case forms the free end of the embryo.

The middle cell of the three divides by further transverse walls, forming, after some longitudinal divisions have taken place, the groups marked *st* and *r* in Fig. 90.

The group of cells marked *st* is a very important one, for from the cells on one side of this group arises the growing point of the stem, which in Monocotyledons

is a lateral structure. The group marked *r* forms the hypocotyl and root, and also contributes something to the suspensor.

The form of the more advanced embryo, after a great many cell-divisions have taken place, is shown in Fig. 91. Towards the top of this figure we see the radicle (*r*), with its growing point directed towards the micropyle (*m*). On one side of the embryo is a depression, in which the lateral growing point of the stem (*g.p.*) is situated. All the part beyond this is the cotyledon (*c*), which at this stage occupies more than half the entire length of the embryo.

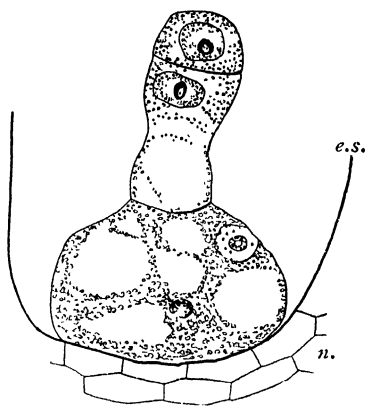


FIG. 89.—Very young embryo of *Alisma Plantago*, a Monocotyledon. *n*, cells of nucellus; *e.s*, membrane of embryo-sac. The embryo with its suspensor consists of three cells, the basal cell being very large. Magnified about 500 diameters.

The essential differences, then, between the embryo of a Monocotyledon and that of a Dicotyledon are these. In the Monocotyledon there is a single terminal cotyledon, and the apex of the stem is lateral, while in the Dicotyledon there are two lateral cotyledons, with the terminal apex of the stem between them. These distinctions are on the whole constant, in spite of great variations in the embryology of both Classes.

The dimensions of the embryo in the Lily, as compared with the whole seed when ripe, are shown in Fig. 91. At the stage figured the chief systems of tissue in the young plant are already marked out. The

embryo now enters on a period of rest. Its further development is postponed until the germination of the seed, and will be described below. In the meantime we must shortly consider the changes which take place in other parts of the ovule during its conversion into a seed.

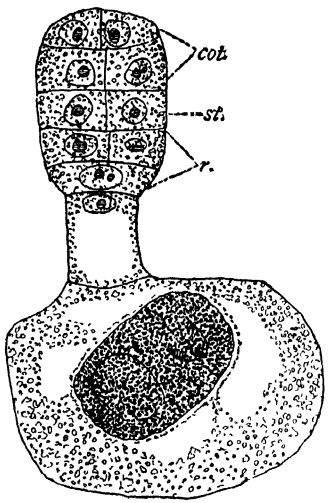


FIG. 90.—Older embryo of same, seen in section. The basal cell is still larger than before. Its enormous nucleus has two nucleoli. *cot*, cells which will form the cotyledon; *st*, disc of cells from one side of which the stem arises later; *r*, radicle. Magnified about 500 diameters.

g. Endosperm

In the Lilies the union of the two polar nuclei of the embryo-sac takes place comparatively late—in fact, not till after they have been joined by the male, vermiform, nucleus from the pollen-tube (Fig. 86). The further changes about to be described, leading to the formation of the endosperm, only take place if this curious process of fertilisation has been accomplished. The development of the endosperm usually starts before that of the embryo.

The triple nucleus of the embryo-sac divides, but without any formation of cell-wall between the daughter-nuclei. The division is repeated again and again in the same manner (see Fig. 87). Soon the nuclei thus formed arrange themselves in the layer of cytoplasm lining the wall of the sac, and there they still go on dividing. All this time the embryo-sac is increasing enormously

in size, and the increase in the number of the nuclei keeps pace with its growth (see Fig. 88). For a long time no cell-walls are formed between them. They lie scattered in the undivided cytoplasm. Only after hundreds of free nuclei have been produced does tissue-formation begin. Then for the first time cell-walls make their appearance between the nuclei, so that the

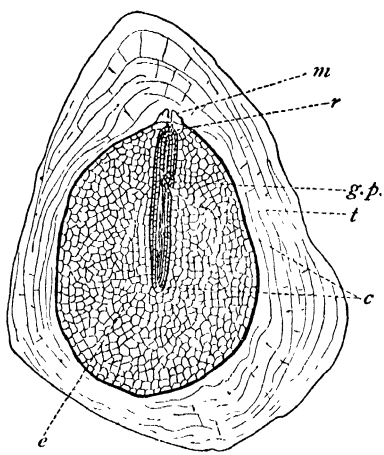


FIG. 91.—Longitudinal section of the ripe seed of a Lily. *t*, testa; *m*, micropyle; *e*, endosperm, in which the embryo is embedded; *r*, radicle of embryo; *g.p*, growing point of stem; *c*, cotyledon. Magnified 6½ diameters. (R.S.)

protoplasm is partitioned up into as many distinct cells as there were free nuclei before. The endosperm tissue, as we may now call it, at first forms a single layer lining the sac. Growth and cell-division, however, go on continuously, until by the time the seed is ripe the whole cavity of the sac, except the small part

occupied by the embryo, is filled by a mass of endosperm (see Fig. 91). Its cells contain reserve starch and proteins, and have very thick cell-walls. The whole tissue forms a great storehouse of food, from which the young plant can draw supplies during germination, before it is ready to shift for itself. This is the most striking difference between the seeds of the Lily and of the Wallflower: in the latter the greater part of the endosperm is a transitory and unimportant structure, which is used up long before the seed is ripe; in the Lily it forms a massive tissue constituting the bulk of the ripe seed, and is only consumed during germination. The Lily thus has a typically *albuminous* seed, while the Wallflower is nearly, though not quite, *exalbuminous*. As regards the presence or absence of endosperm in the ripe seed, there is no constant difference between the two Classes. While, as we have seen, a large number of Dicotyledons have albuminous seeds, many Monocotyledons are exalbuminous, as, for example, the Orchids and the Water-plantains. From one of the latter (*Alisma Plantago*) our Figs. 89 and 90 were taken. In both Classes a majority of the members have albuminous seeds, and in almost all there is at least a temporary formation of endosperm.

The albuminous seeds of some of the Monocotyledons have great practical interest. In Wheat, Rye, and the other grains, it is the endosperm of the seed from which flour is prepared. In fact, when we eat bread, we are converting to our own use the stores of food which the Wheat or Rye plant had provided for the benefit of its seedlings.

h. The Ripe Seed and Fruit

The seeds of the Lilies are arranged in six rows in the fruit, two rows in each compartment; they are packed very close together, and are flattened, so that each row has somewhat the appearance of a pile of coins (Fig. 92, *s''*). Fig. 91 shows the section parallel to the broad side of the seed. Each seed has a firm, thick testa, formed from the two integuments of the ovule, the outer of which constitutes the thicker and harder layer.

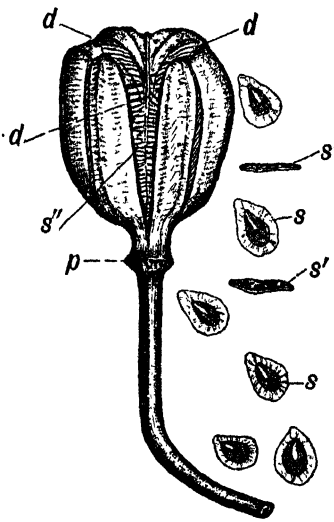


FIG. 92.—Ripe capsule of a Lily (*L. pyrenaicum*) seated on the pedicel. The capsule is dehiscing by three longitudinal splits (*d*), each corresponding to the middle of a carpel. On the right are seen the seeds being shed; *s*, seeds in surface view; *s'*, from the edge; *s''*, seeds still contained within the capsule. For the seeds, cf. Fig. 91. *p*, ridge of receptacle, from which the perianth has fallen. ⅔ natural size. (R. S.)

The ripe seed, therefore, consists of three essentially different structures: (1) the embryo, developed from the fertilised ovum; (2) the endosperm, or tissue formed inside the embryo-sac, also in consequence of an act of fertilisation; (3) the testa, formed from the integuments of the ovule (Fig. 91). The nucellus has by this time been absorbed.

The point where the seed is attached to the funicle is called the *hilum*, and as the ovule from which the seed was developed was anatropous, it follows that the hilum and the micropyle are close together.

The fruit is called a *capsule*, *i.e.* it is *syncarpous*, *dry*, and *dehiscent*. The structure shows very little difference from that of the ovary, but there is an enormous increase in bulk, and some change in shape and texture, the fruit being thicker in proportion to its length than the ovary, while its tissues have become harder (Fig. 92). The style withers away during the ripening of the fruit. The increase in size of the ovary in becoming the fruit is a consequence of the fertilisation of the ovules, but how exactly this influence is brought to bear on the ovary is unknown.

The opening or *dehiscence* of the capsule to set free the seeds takes place by three longitudinal splits, one running along the middle of the outer wall of each compartment throughout its whole length (Fig. 92, *d*). The fruit is thus cleft into three divisions, each representing two half-carpels. The flat, light seeds are well adapted to being scattered by the wind, as they are shed from the dehiscent capsule (Fig. 92).

i. Germination

The organ which grows most actively in the early stages of germination is the cotyledon, which elongates to an enormous extent, attaining a length of several inches. The radicle is first pushed out through the micropyle, and then grows down into the earth. The tip of the cotyledon remains immersed in the endosperm, and acts at first as an absorbing organ, by means of which the food substances in the seed are

taken up by the young plant. The cellulose, starch, and proteins of the endosperm have to be rendered soluble before they can be absorbed. This is brought about by means of various *enzymes*, which are probably secreted by the tip of the cotyledon (p. 216).

In its lower, sheathing part the cotyledon encloses the bud of the stem, and below this again are the rudimentary hypocotyl and the main root, which is developed from the radicle and grows straight downwards. Henceforth the seedling is able to provide its own mineral food. The seed-coat is lifted high above the ground on the tip of the cotyledon, which becomes a long narrow green leaf, and thus constitutes the first assimilating organ of the seedling (see Fig. 93).

The young stem develops into the bulb, the first bulb-scale being formed by the sheath of the cotyledon. Other scale-leaves are soon formed from the

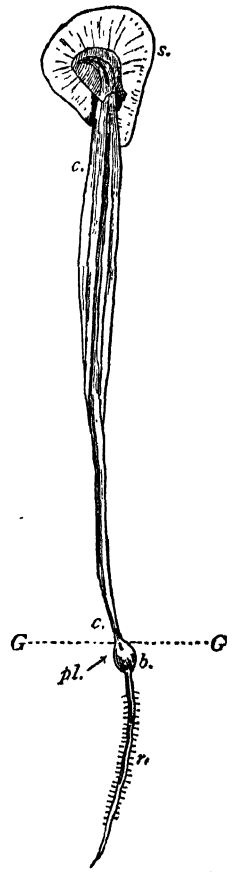


FIG. 93.—Young seedling of a Lily (*L. giganteum*). *r*, main root; *c*, cotyledon; *b*, base of cotyledon, forming first scale of bulb; *pl*, arrow pointing to plumule, now hidden, which will grow out through the crevice in base of cotyledon; *s*, seed-coat, still attached to tip of cotyledon; *G...G*, level of ground. Natural size. (R. S.)

growing-point. The bulb appears at first as a lateral growth at one side of the base of the cotyledon. The main root may attain a length of a couple of inches, but it sends out few, if any, rootlets. Its function is only temporary, for it is soon replaced by adventitious roots arising from the base of the bulb. After a time the bulb sends up green foliage-leaves (Fig. 94); the cotyledon decays, leaving only its base; the seed, the endosperm of which is now exhausted, is reduced to an empty shell, and germination is now ended.

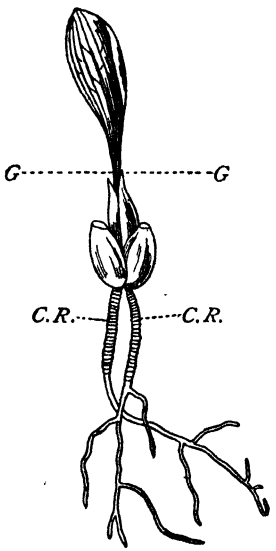


FIG. 94.—Seedling of a Lily (*L. pardalinum*) in its second year, bearing a foliage-leaf. *C.R*, contractile adventitious roots, showing transverse wrinkling; *G*...*G*, level of ground. Natural size. (R. S.)

In some Lilies, and in many other plants, both Monocotyledons and Dicotyledons, the base of the stem is brought to its proper depth in the ground by the contraction of the roots. In *L. Martagon* the young bulb of the seedling is gradually drawn down year by year, owing to the shortening of the adventitious roots. As the end of the root attaches itself firmly to the soil, the effect of the contraction is to exert a downward pull on the bulb. The upper part of the root is alone capable of contraction, and is much thicker than the rest. The

inner cortex is the actively contractile tissue; as it contracts the external layers are thrown into transverse wrinkles, as shown in Fig. 94. New roots of this kind are formed each year, until the bulb has reached its normal depth (three inches or more in the case of *L. Martagon*).

Summary

If we now shortly sum up those essential points in the life-history of the Lily in which it serves as a type of the Monocotyledons generally, we find that the following are the chief:—

(1) In the external morphology the most striking point is the predominance of adventitious roots, the main root serving a merely temporary purpose, namely, the nutrition of the seedling. The explanation of this peculiarity is to be found in the mode of growth of the plant as a whole. The main root is a slender structure, corresponding to the small dimensions of the thin basal portion of the stem, with which it develops simultaneously. Hence, as the stem becomes for a time larger and larger in each successive node and internode, the root becomes more and more inadequate to supply its needs. The root has no secondary growth in thickness, and therefore cannot make good its deficiencies. Thus the requirements of the plant can only be satisfied if the later-formed bulkier portions of the stem produce new and larger roots proportioned to the organs which they supply.

(2) The primary bundle-system in the mature stem and its adventitious roots is on the whole more complex than in Dicotyledons, the individual bundles being more

numerous, and their course, in the stem, at any rate, less simple. In the leaf we have, as a rule, what is called "parallel venation," which means that there are a number of large longitudinal bundles with more delicate transverse connections. The presence of numerous main bundles in the leaf goes together with the complex conducting system of the stem. In many Monocotyledons the leaf-bases are broad, with numerous bundles entering them from the stem, though this does not apply to the White Lily.

(3) The closed structure of the vascular bundles, and the general, though not universal, absence of secondary thickening in Monocotyledons, have been sufficiently dwelt upon above. These characters render necessary the greater complexity of the primary tissues, and also explain the absence of a persistent tap-root, which without cambium cannot satisfy the needs of the plant as it grows in bulk.

(4) Perhaps the most constant character of all is found in the structure of the embryo, with its single terminal cotyledon and lateral growing-point. It is this peculiarity, more than any other single character, which separates the Monocotyledons from the Dicotyledons as a distinct Class. We have now considered the distinctions between the two Classes; their points of agreement scarcely need to be emphasised.

The general morphology is alike in both: stem, leaf, and root show the same distinctive characters, both internal and external.

The structure of the tissues, as distinguished from their arrangement, is similar in the two Classes.

The most striking agreement, however, is in the floral organs. Speaking broadly, we may say that

there are *no* characteristic differences between the two Classes here. Their similarity is equally marked, whether we consider the general plan of the flower, the structure of its several organs, or the minute details of their development. Apart from one or two trivial and not very constant differences, we may say that every detail in the development of the perianth, of the stamens, of their pollen-sacs and pollen, of the pistil, the ovules, the embryo-sac and the endosperm, as well as the process of fertilisation, shows the most minute correspondence in both Classes. In fact, so close is the agreement in all important characters, that if we want to find a ready means of distinguishing these Classes by their flowers, we have to fall back on arithmetic, and make what use we can of the rule that in Monocotyledons the parts of the flower are usually in threes, and in Dicotyledons in fours or fives!

On the whole, we may say that the points of agreement between our first two types much outweigh the points of difference.

The classes Dicotyledons and Monocotyledons together constitute the sub-kingdom *Angiosperms*, characterised by the fact that the ovules are contained within a closed ovary, and that consequently fertilisation has to take place through the intervention of a stigma.

CHAPTER III

Outlines of Physiology

In studying our first two types we have obtained a general idea of the form and structure of the root and shoot in green plants. We have also learnt something as to their functions. It will be well for us, however, before proceeding further, to endeavour to gain a more connected view of the mode of working of the vegetative organs. We have to learn what food the plant needs; from what sources its various kinds of food are obtained; what changes they have to undergo in order to be made use of by the plant; we have also to inquire how plants breathe; and generally, what are the actions which a plant carries on as a living organism. All these are physiological questions, for we have already learnt that physiology asks what is the work done by plants and their organs. We shall only attempt here to give a very short and simple answer to these inquiries; anything like a full answer would require an advanced knowledge of physics and chemistry, which we must not take for granted. A little elementary knowledge of these two subjects is indeed absolutely necessary, if we wish to understand even the simplest facts about the life of plants.

I. *The Food of Plants.*—The first step necessary in order to understand anything about the nutrition of plants is to learn what chemical elements a plant contains. Probably most of the elements which exist

have been detected at some time or other in plants; those, however, which are *constantly* present, are only thirteen in number, namely, carbon, hydrogen, oxygen, nitrogen, sulphur, phosphorus, potassium, calcium, magnesium, iron, sodium, chlorine, and silicon. But although these elements are very constantly found, on chemically analysing green plants, it does not follow that they are all necessary to the life of the plant. Many of them we know to be so, because they enter into the chemical composition of the substances of which the tissues of the plant consist. For example, the three elements, carbon, hydrogen, and oxygen, constitute cellulose and starch; the proteins, of which the cytoplasm is composed, contain, in addition, nitrogen and sometimes sulphur; while phosphorus is regularly present in the substance of the nucleus. As regards the other seven elements, analysis does not tell us whether they are necessary to the life of the plant, or whether they may not be taken up simply because they are present in the soil.

This question can only be answered by experimental cultures, so arranged that we know exactly what chemical bodies are supplied to the plant.

The simplest method is by means of cultivation in water. We must take care that the water used is pure to begin with, and therefore carefully distilled water must always be chosen. To this water we add small quantities of the chemical compounds with which we wish to experiment. These compounds when in solution are broken up into *ions*, *e.g.* potassium nitrate (KNO_3) in water becomes dissociated into potassium (K) and

nitrate (NO_3) ions. Hence the same four types of ions will be present in a solution of potassium nitrate (KNO_3) and sodium chloride (NaCl) as in a solution of potassium chloride (KCl) and sodium nitrate ($NaNO_3$). In the dilute solution used in water cultures the salts are practically completely dissociated. It is in the form of ions that the substances dissolved in the water pass into the plant. It will be well to choose such compounds as are known to be present in a natural soil.

We may begin with a food-solution composed thus :—

Water (H_2O)	1000 cubic centimetres
Potassium nitrate (KNO_3)	1·0 gram
Sodium chloride (NaCl=common salt) . .	·5 gram
Calcium sulphate ($CaSO_4$)	·5 gram
Magnesium sulphate ($MgSO_4$)	·5 gram
Calcium phosphate ($Ca_3(PO_4)_2$)	·5 gram
Iron chloride (Fe_2Cl_6)	a trace

It will be seen that the amount of the various salts is very small in comparison with the bulk of water. Plants in nature take up their food, in so far as it is supplied by their roots, in very weak solutions.

A seed (say, of the Maize, or Bean, or Pea, or Buckwheat) is allowed to germinate in damp sawdust. The seedling is washed in distilled water, and is then fixed in a split cork fitted into a wide-mouthed bottle, with its root dipping into the food-solution with which the bottle is filled. We have spoken of a food *solution*, but one of the salts, calcium phosphate, is only very slightly soluble in water, and most of it will remain as a powder at the bottom of the bottle.

Now, in a water culture of this kind, the young

plant will remain healthy and continue to grow; it will even in time flower and ripen its seed. In fact, under these artificial conditions, the plant may be brought successfully through its entire life-history, while the amount of its organic substance is increased, it may be several hundredfold, as compared with the quantity contained in the seed to start with. The success of this experiment proves that the compounds presented to the plant contain all that is necessary for its nutrition. Yet, among the elements contained in the water and salts of the food-solution, one is conspicuous by its absence; we have given the plant no carbon whatever. We know, however, that the *dry-weight* of a plant—that is to say, its weight after evaporating the water which it contains—is half made up of carbon. We know also that every organic substance—cellulose, starch, sugar, protein, or anything else which goes to build up an organism—is a compound of carbon; we know, then, that as the organic substance of a plant has increased some hundredfold, so also has its carbon increased in like proportion. Our specimen, then, has obtained abundant carbon, but not from the food-solution, and therefore not by means of its roots. The only remaining source is the atmosphere, and the carbon can only have been obtained by means of those organs which are exposed to the air, namely, the leaves and stem.

We will return later to the question how the plant obtains its carbon; our immediate object is to determine which of the other elements are essential. It will be noticed that no compound of silicon was

added to the water, and this element certainly cannot be obtained from the air. Some trifling quantity might possibly be derived from the glass of the bottle, but the amount to be thus obtained is too small to be of any importance. We infer, then, that silicon, in spite of its general presence in plants, is *not* essential to their nutrition. This does not prove that it is of no use. To many plants, such as grasses, silicon is of great importance in hardening the outer surface of the epidermis, and thus rendering it a better protection against parasites, but *as food* silicon is not necessary to the plant.

Of the salts offered to the plant, sodium chloride can easily be proved not to be essential. If it is left out altogether, the plant will still flourish and come to maturity. The sodium, then, can certainly be dispensed with. It is said that for some plants chlorine in some form or other is needed, but certainly this is not the case with most; yet these two elements are constantly present in plants, simply because they are constantly present in the soil.

If, however, we omit any of the other elements from our food-solution, the plant suffers. Suppose, for example, that no compound of iron be added to the water; for a time the seedling grows normally; the new leaves which are formed, however, are not green, but yellowish—in fact, they contain no true chlorophyll.[1] Hence no assimilation of carbon can take place, and no further increase in the organic substance of the plant can be produced. The reason why the first few

[1] See footnote, p. 33.

leaves are green is that a certain amount of iron is contained in the seed. The disease caused by the want of iron is called *chlorosis*, which means pallor, and is very easily cured. If a few drops of a solution of an iron salt be added to the water, the pale leaves soon begin to turn green, and the same result is produced if the surface of the leaf be painted with the dilute iron compound. It is very important to add no more iron than is necessary. In quantities sufficient to colour the water it is poisonous to the plant. The way in which iron is necessary is thus made quite clear. Without iron no true chlorophyll can be formed.

The necessity for the six elements which are known to enter into the composition of the tissues is self-evident, and is easily proved experimentally. Suppose, for example, that we wish to determine whether phosphorus is essential. All we have to do is to leave out the calcium phosphate and substitute for it the same quantity of calcium sulphate. The growth of the seedling soon ceases—as soon, in fact, as the phosphorus in the seed has been used up. In like manner we can prove the necessity for the other tissue-forming elements.

The presence of potassium, calcium, and magnesium is also essential. If we substitute sodium nitrate for potassium nitrate, the seedling stops growing; and the same is the case if we replace the calcium and magnesium compounds by those of any other metals. These elements are in some way or other necessary for the process of assimilation; in their absence the

formation of new organic substance is checked. Their exact mode of action, however, is uncertain, although magnesium is known to be an essential constituent of true chlorophyll.

We learn, then, by this method of water culture that the *essential* elements for the nutrition of a green plant are only ten in number, namely, carbon, hydrogen, oxygen, nitrogen, sulphur, phosphorus, potassium, calcium, magnesium, and iron.

Something must be said about the source of nitrogen. Nitrates, such as potassium nitrate, are, as we have seen, quite successful as a source of nitrogen to the plant. If we use ammonium compounds, such as ammonium phosphate ($(NH_4)_3PO_4$), instead of nitrates, the plant will also flourish, but it is possible that in this case the ammonium compound is converted into a nitrate before being made use of. If, however, we leave out nitrogen compounds from the food-solution altogether, most plants will starve. Yet we know that the atmosphere consists of $\frac{4}{5}$ of nitrogen to $\frac{1}{5}$ of oxygen, approximately. In most cases, then, the free nitrogen of the air cannot be assimilated by plants. It is known, however, that there are important exceptions to this rule; plants of the Pea family (Leguminosæ) for example, are able, under certain conditions, to supply their demand for nitrogen entirely from the air, while no nitrogenous compounds are offered to their roots. The conditions under which this takes place, however, can only be understood after we have made ourselves acquainted with some of the simplest vegetable organisms, for it is only by the help of certain Bacteria living in their roots that leguminous plants can make use of

atmospheric nitrogen, and so enrich the soil for future crops.[1]

II. *Assimilation of Carbon.*—We will now consider the question how a plant containing chlorophyll obtains its supply of carbon, the most important of all the elements for nutrition. We have already learnt that the plant certainly does not obtain this element by its roots, and that the air is the only source of carbon available.

Now, the atmosphere contains carbon in the form of carbon dioxide, more commonly, though inaccurately, called carbonic acid.[2] The proportion of this gas contained in the air is very small, amounting only to about three volumes in 10,000 volumes of air. Yet from this relatively small amount the entire supply of carbon for most green plants is obtained.

Carbon dioxide is formed whenever carbon is completely burnt, or, in other words, completely oxidised. It contains the maximum amount of oxygen with which carbon can combine. Now we know that the substance of plants is combustible; in fact, all our fuels are directly or indirectly of vegetable origin. It follows, then, that the tissues of plants must be comparatively poor in oxygen, or they would not burn. Hence we see that the carbon dioxide of the air must lose the whole or part of its oxygen when it is assimilated by a plant.

[1] See Part II. (*Flowerless Plants*), p. 284.

[2] Carbonic acid is, properly speaking, the compound of carbon dioxide with water, and has the formula H_2CO_3. Hence carbon dioxide is sometimes called carbonic *anhydride*, the latter word implying that the acid is deprived of its water.

That green plants in sunlight give off oxygen is easily proved. Some pieces of any green water-plant (such as the *Elodea*, mentioned on p. 41) are put into a glass of ordinary water, which always contains some carbon dioxide in solution. The glass with the Water-weed in it is allowed to stand in a sunny place, and we soon see that bubbles are given off from the plant in a constant stream. If we catch these bubbles, as they rise to the surface, in an inverted test-tube filled with water, we find that they consist chiefly of oxygen, as can be easily shown by plunging a glowing match into the gas thus collected ; the match will at once catch light again. If, however, the plant be placed in water which has been previously deprived of its carbon dioxide by boiling, no oxygen will be given off.

If a plant, or simply some green leaves, be placed in a bell-glass, dipping into mercury below, and containing a measured quantity of carbon dioxide, and left for some time exposed to light, the volume of the gas in the jar remains unaltered. If the gas be analysed after some hours, the carbon dioxide will be found to have diminished, and the oxygen to have increased, and in fact the volume of carbon dioxide lost will be exactly equal to the volume of oxygen gained. In other words, the plant has given out exactly as much oxygen as it has absorbed carbon dioxide. It is likely that half of the oxygen evolved is derived from the carbon dioxide, and half from the water with which the carbon dioxide enters into combination in the process of carbon assimilation.

The decomposition of so stable a compound as

carbon dioxide is a very difficult process to carry out in the laboratory. Thus, in order to decompose carbon dioxide by heat, a temperature of no less than 1300° C. is required. Yet decomposition of carbon dioxide is carried on by the green plant at the ordinary temperature of the air—say 10° to 30° C. The energy which enables a green leaf to do its work is derived from the rays of the sun; plants will only assimilate carbon in the light.[1] This is easily proved; if we repeat the experiment just described in a dark place, no carbon dioxide is absorbed, and no oxygen is set free. Other sources of light may be substituted for the sun. Thus, plants will assimilate actively and continuously when exposed to the electric light. As in nature sunlight alone is in question, we may say that all the organic material of the world, all the animal and vegetable substance which it contains, has been directly or indirectly produced through the assimilation of carbon from carbon dioxide by green plants in sunlight. There are not many rules in science without an exception: it has lately been shown that certain very simple organisms are able to obtain their carbon from inorganic sources without the help of light; the amount of organic substance thus formed, however, is too small to affect our statement appreciably. It is only green plants, and parts of plants, which can decompose carbon dioxide in sunlight. If we had used for our experiments coloured or white flowers, or colourless roots, or any part of a plant containing no chlorophyll, we should have found that no absorption of carbon dioxide or evolution of oxygen

[1] Hence carbon-assimilation is now often termed *photosynthesis*.

took place. It is not necessary that the plants should appear green externally, it is enough that they contain chlorophyll. For instance, the leaves of the Copper Beech are of a brownish-red colour, yet they assimilate like ordinary green leaves, because they contain chlorophyll, which, however, is disguised by the presence of a red colouring matter (anthocyanin) in the sap.

We already know that chlorophyll is contained in the protoplasmic chlorophyll-corpuscles or plastids. The whole apparatus is necessary for the work to be done; the chlorophyll is useless for the purpose of assimilation without the protoplasmic plastid, and the plastid cannot assimilate without the chlorophyll. We are not at all clear at present as to the special duties performed by the two partners. Most probably the chlorophyll serves to catch certain rays of light, by the energy of which the plastid is enabled to do the work of decomposing carbon dioxide and water. It has been proved that the red rays of light are the most active in promoting carbon-assimilation. The absorption spectrum of chlorophyll shows a conspicuous dark band in the red. Hence we know that these red rays are absorbed by the chlorophyll, and do not pass through it as light. It is very probable that it is the energy of these absorbed rays which is employed on the work of assimilation.

We have now seen that carbon-assimilation is dependent on light; it is also dependent on temperature. Although all other conditions may be favourable, yet if the temperature be too low no assimilation takes

place. Thus, in our experiment with the *Elodea*, we should find little or no oxygen given off unless the temperature of the water was at least 6° C. The minimum temperature varies very much for different plants, but for every plant there is a certain temperature below which no carbon dioxide can be decomposed.

Light is not only necessary in order that the chlorophyll-containing organs may perform the work of assimilation, but also for the formation of chlorophyll. Although the plastids are always present, the pigment chlorophyll is not formed in them in the absence of light. If a Potato plant be grown in the dark, it remains a yellowish colour in the absence of the two green pigments from the mixture of pigments which we have called chlorophyll (see p. 33). We must be careful to distinguish between these two actions of light, which are quite distinct: a plant will become green in the light even though it be kept in air containing no carbon dioxide, so we see that assimilation is not necessary for the production of chlorophyll, though the presence of chlorophyll is one of the necessary conditions of assimilation.

A green plant kept in the dark cannot decompose carbon dioxide, and therefore under these circumstances it forms no new organic substance. A potato kept in a warm and damp but dark cellar will often grow. It produces a pale, unhealthy plant, with long stems and small leaves. If such a plant be dried and weighed, we find that its solid substance is not

greater, but rather less, than that of the tuber from which it has developed. It has grown entirely at the expense of the food-substances ready stored in the tuber; a great deal of water has been absorbed, but no new organic substance has been formed; on the contrary, some has been lost, for a reason which we shall explain presently. The plant, in fact, has earned nothing, but has been living on its capital, and has naturally become poorer by doing so.

The same thing would happen if a plant were allowed to grow in the light, but in an atmosphere destitute of carbon dioxide. For the purpose of this experiment the specimen is grown under a bell-glass, into which air is admitted through a tube, containing pieces of pumice-stone soaked in a solution of caustic potash (KOH). The potash absorbs the carbon dioxide, so that none reaches the plant. Here also the result is that no fresh organic material is formed; if the plant grows at all, it does so at the expense of the food-substances which it had previously stored up.

We may sum up our conclusions up to this point as follows:—

Green plants, as a rule, obtain all their carbon by the decomposition of the carbon dioxide of the atmosphere.

Consequently, in the absence of carbon dioxide, no fresh organic substance is formed. The decomposition of carbon dioxide can only take place under the action of light (the red rays being the most effective) and at a sufficient temperature.

It can only be performed by those parts of plants which contain chlorophyll in their plastids.

This process of the assimilation of carbon from carbon dioxide may fairly be considered the most important of all physiological phenomena, for on it the whole existence of plants and animals is dependent. Herbivorous animals eat plants, and are in their turn eaten by carnivorous animals and by man. Our own life, and that of the whole animal kingdom, would thus be absolutely impossible without the work done by the chlorophyll-corpuscles of plants.

We will now inquire what becomes of the carbon after it is taken up by the plant. We know in a general way that it is employed with other elements to build up the protoplasm, starch, cellulose, and other bodies of which a plant consists. Can we trace the stages of the process? Our knowledge here is still very imperfect, but yet something has already been made out.

The facts are that carbon dioxide and water are converted eventually by the chloroplasts under the influence of light into carbohydrates, with the evolution of oxygen. A simple suggestion from the chemical standpoint has been made that in the first place carbon dioxide and water combine to make formaldehyde (CH_2O), as indicated in the following equation—

$$CO_2 + H_2O = CH_2O + O_2.$$

It is further suggested that the formaldehyde is converted into a sugar, *e.g.* one having the formula $C_6H_{12}O_6$, which is the same formula as that for glucose, thus—

$$6\,CH_2\,O = C_6H_1O_6.$$

On exposure to light the formation of sugar commences, the concentration of sugar in the mesophyll cells rises, and the rate of diffusion of sugar from the cells also increases. In many plants starch appears in the plastids when a certain concentration of sugar is attained.

In some plants, *e.g.* sugar-cane, starch is never found under natural conditions. That this is due, not to any inherent inability of the protoplasm to form starch, but to the sugar-concentration never reaching a sufficiently high level, is shown by the fact that starch formation can be induced in such a plant by placing the tissues in a strong sugar solution.

The change from sugar to starch is a reversible one. On the coming of darkness, when sugar formation by photosynthesis ceases, the diffusion of sugar away from the mesophyll cells continues for some time and more sugar is produced at the expense of the starch. When the concentration of sugar has fallen to a certain level all the starch will have disappeared from the plastids. This concentration is practically the same as that at which starch formation began to take place during photosynthesis. Although under some conditions the amount of starch increases and under other conditions decreases in the mesophyll cells, there are reasons for supposing that the formation of starch from sugar and the formation of sugar from starch take place side by side, the net result depending upon which of the processes is the faster.

It must be clearly understood that there is yet no exact proof that formaldehyde is first formed in the

process of photosynthesis. If it is so formed, it must be *immediately* converted into some other compound, *e.g.* a sugar, as formaldehyde itself is poisonous to plants. Many kinds of sugar have been made in recent years by chemists from inorganic compounds in the laboratory, and it is an interesting fact that bodies of the nature of aldehydes are important links in the chain of reactions by which sugars have been artificially produced.

Starch is an insoluble form of carbohydrate, which is convenient for storing purposes. Both in the chloroplastid and in the leucoplastid starch is produced at the expense of sugar. The difference between them consists in the origin of the sugar, which in the former case is the result of the assimilation of inorganic compounds, while in the latter it is derived from previously existing carbohydrates.

If starch is formed, it has to be rendered soluble, in order to be transportable to the other parts of the plant. It is well known that starch can be converted into sugar by means of an enzyme called *diastase*, which is derived from the protoplasm, and is found, for example, in large quantities in germinating seeds, such as those of Barley during the process of malting. It has been proved that diastase is present in the leaf, and serves to convert into sugar the starch which is formed in the chlorophyll-corpuscles.

The soluble carbohydrates are transported chiefly through the parenchyma, and especially through that part of it which immediately accompanies the vascular bundles. They may either be conducted directly to

the seats of growth, such as the apical growing points, or the cambium, to be employed chiefly in the formation of new cell-walls, or they may be conveyed to organs which serve as storehouses of reserve food, such as the endosperm or the cotyledons in a seed, the tuber of a Potato, or the root of a Turnip. In these regions the sugar is very often reconverted into starch by the leucoplasts; it may, however, be stored up in a soluble form, as inulin in the Dandelion, or cane-sugar in the Beet. In some cases it is employed to form enormously thick cellulose walls, as in the endosperm of many Palms; these cell-walls are dissolved again on germination, and so rendered available as food for the seedling. In other cases, again, as in oily seeds, the non-nitrogenous food-materials are stored, not as carbohydrates, but as fatty oils.

We know little or nothing at present about the first formation of *proteins* in the plant. It is most probable that, like the carbohydrates, they are first formed in the leaves. In addition to carbon, hydrogen, oxygen, and nitrogen, sulphur also often enters into their composition, while the chromatin of the nucleus further contains phosphorus. The three elements last named are, as we have seen, taken up in the form of various ions with the water absorbed by the roots. It appears probable that the proteins formed in the assimilating tissue are taken up by the phloëm-cells at the ends of the vascular bundles, and it has commonly been held that they are conveyed to other parts of the plant through the sieve-tubes. We often find the

proteïns stored up in the form of definite granules, such as the aleurone-grains, which occur very generally in seeds (see p. 38).

III. *Absorption.*—We have now obtained some idea of the chief nutritive processes of a chlorophyll-containing plant, but we have still to inquire how the various food-substances are absorbed.

It is by way of the stomata that the bulk of the gaseous interchange between the green parts of plants and the atmosphere takes place. During photosynthesis the carbon dioxide dissolved in the water contained in the mesophyll cells is used up ; more carbon dioxide dissolved in the wet walls surrounding the cells passes into the cells to take its place ; in turn more carbon dioxide in the intercellular spaces of the mesophyll becomes dissolved in the wet cell walls, and this is replenished from the external atmosphere. Although illustrated by a step-to-step process, in reality there is a constant stream of carbon dioxide passing from the outside atmosphere through the stomata into the chloroplasts within the mesophyll cells.

The extremely small size of the stomatal pores, through which the gases have to pass, may seem a difficulty, but it has recently been proved that the rate at which a gas will diffuse through an opening varies, not with the *area* of the opening, but with its *diameter*. Hence a large number of minute pores is far more effective as a means of diffusion than a smaller number of larger pores, and the conditions in the epidermis of a leaf prove to be specially favourable for a relatively rapid passage of gases.

The mineral substances taken up by the root are absorbed through the root-hairs, where these are present, and must be taken up in solution. Yet we know that many plants flourish well in a comparatively dry soil. In such a soil, however, each particle of earth is surrounded by a film of water, which adheres to it firmly. The root-hairs attach themselves to such particles, and are thus enabled to absorb a part of the watery film which surrounds them (see Fig. 29, p. 77). The root-hairs, however, are not dependent entirely on salts which are ready dissolved in the water of the soil. They are able to dissolve other compounds for themselves. Calcium phosphate, for example, is only soluble to a very small extent in water. The root-hairs, however, give off carbon dioxide in solution, by which minute quantities of salts are dissolved, and can then be absorbed as ions. This solvent action of the root-hairs can be proved by growing plants in a thin layer of earth covering a slab of polished marble. After some time, an exact print of the course of the roots will be found on the smooth surface of the marble, which has become corroded wherever the hairs of the roots have been in contact with it.

The passage of water into a root-hair has been explained on purely physical grounds. If water containing substances in solution is separated from pure water by a membrane, *e.g.* parchment, which lets water pass through, then water will tend to pass into the solution, the *attraction* of the solution for the water being greater the stronger the solution. In a root-hair the concentration of substances dissolved in the

cell-sap is usually greater than that in the surrounding soil water. Hence the cell-sap tends to draw water from the soil through the cell-wall and protoplasmic lining of the cell. As water passes into such a cell, the cell-sap increases in volume and exerts an outward pressure on the cell-wall. This is stretched and presses inwards on the cell-sap. As more water passes in and the stretching increases, a point is reached at which the inward pressure of the wall (wall pressure) just prevents the further entrance of water, although the concentration of substances dissolved in the cell-sap is still greater than that in the soil water. In the cell adjoining the root-hair there are also substances in solution in the cell-sap. This cell tends to draw water from the root-hair in the same way that the root-hair does from the soil. As the adjoining cell draws water from the root-hair, the wall pressure of the latter decreases, and so the root-hair can now draw more water from the soil to make up for that lost to the adjoining cell. *In this way the root-hair acts as a channel for the water from the soil to the cell adjoining the root-hair.* This adjoining cell continues to take up water *via* the root-hair until its wall is stretched to the point at which further passage of water is prevented. In this way we can proceed all over the plant. Since the chain of cells between any one cell and the soil merely acts as a way for the passage of water, the chain could be replaced by a column of water in a tracheid or even a wet tracheid wall. It should be realised that there are many channels from the soil water to any one cell, so that other paths remain open even if one is rendered

unavailable, *e.g.* if a tracheid becomes empty or its walls dry.

When the plant is losing no water all the living cells have their walls stretched to the point at which no more water can be drawn from the soil. When, however, water is lost in transpiration by a mesophyll cell of a leaf, the wall pressure decreases and so the cell can now draw water from its neighbouring cells. The wall pressure in these is reduced and they can draw water from more remote cells, and so on, until the soil is reached. This goes on continuously and not step by step. It is rather like the start of a train in which the trucks are connected by means of iron bars instead of slack chains. In such a train the last truck would start almost simultaneously with the engine. The water passes up to a transpiring mesophyll cell along many paths. Most of it passes along the path of least resistance, which is probably the tracheids and vessels of the vascular system.

We now turn to the passage of salts into the plant. The cell-wall and protoplasm of the root-hairs are permeable to some of the salts in solution in the soil water. The concentration of these, by diffusion, tends to become the same inside the root-hairs as outside in the soil water. As these substances are used up in the growth of the plant, the meristems draw on the surrounding cells, which eventually draw on the root-hairs, into which more of the substances pass from the soil. The concentration, inside the cells, of any one of these substances to which the protoplasm is permeable never reaches that in the soil water until growth

and consumption of this substance ceases. In those parts of the plant such as tracheids, where the solution can move bodily, the salts move along with the water, and hence transpiration, which causes the water movement, will favour the movement of the salts. When there is practically no water movement (*e.g.* into protected buds) the salts move by diffusion only.

IV. *The Ascent of the Sap.*—The ascent of the sap through the plant is a subject which is by no means thoroughly understood at present. There are two distinct processes which have to do with it: one is *root-pressure*, the other is *transpiration*. The water taken up by the root through its hairs is forcibly pumped upwards, as can be easily proved by cutting off the stem or branches of a plant, especially in spring, when the ascent of the sap has begun, and before there is any appreciable loss of water from the surface of the leaves. From the cut stumps of the stem or branches great quantities of water, amounting in some cases to several quarts, are exuded. This has long been observed in the case of the Vine in spring, when it is said to *bleed*. The same thing can be seen at any time during active vegetation, but in the summer the plant is losing water rapidly by its leaves, and consequently the water-conducting tissues are comparatively empty. Under these circumstances it is necessary to wait for a time after cutting off a branch, before the welling-out of water from the stump begins.

This movement of the water is undoubtedly due to the action of the living cells of the root. Through

the root-hairs they take up water from the outside, in the manner explained above. The elastic cell-walls become distended, while the sap within is at a high pressure, which may amount to three or four times the pressure of the atmosphere. The cell-wall is easily permeable by water, and such pressure in the interior of the cell could not be maintained if it were not for the protoplasmic lining by which the entrance and the exit of the water is regulated. Cells or whole tissues which are thus distended by sap are said to be in a *turgid* condition. The turgid parenchyma cannot go on taking up water indefinitely; as fresh supplies are taken in from the soil, a portion of the cell-sap already contained in the tissue is continuously forced out again. The sap thus expelled from the cells under pressure does not leave the plant; it is pumped into the vessels and tracheids of the wood. These elements, as we already know, only contain air at a very low pressure, so that little or no resistance is offered to the sap which enters them. As the process goes on, the column of water in the vessels rises, and when a cut stem bleeds it is from the open ends of the vessels, or tracheids, that the sap escapes.

Under natural conditions, if root-pressure acted alone, the result could only be that all the wood of the plant would soon become completely water-logged. This actually happens in certain cases; after a damp, cool night, when little or no transpiration can take place, we find that the leaf margins of many plants are studded with drops of water, which we might very

easily mistake for dew. If wiped off, however, the drops soon reappear in the same spots, and in fact they come from within, not from without, being excreted by the plant. When a plant is completely gorged with sap, and no transpiration is possible, it gets rid of its superfluous water in the liquid form, and in many plants there are special glands for this purpose.

This state of things, however, is exceptional. In the day-time, under the influence of light and heat, the stomata are active, and through them water is given off in the form of vapour. That this is so is easily proved. If a plant be placed under a bell-glass, the soil in which it is growing being completely covered with tinfoil, so that no evaporation from the earth is possible, we find that dew is soon deposited on the inside of the glass. This dew can only have been produced by the condensation of the aqueous vapour given off by the plant. Under ordinary conditions the air in the bell-glass soon becomes saturated with vapour, and no further transpiration is possible. If, however, we place under the bell-glass some calcium chloride ($CaCl_2$), or other substance which absorbs water vapour, we can obtain a measure of the transpiration of the plant, for the increase in weight of the calcium chloride in a given time is due to the water which it has absorbed and which was previously transpired by the plant. The quantity of water given off by transpiration is very large, amounting, as has been calculated, to from 50 to 100 litres a day in the case of a large tree.

Now, this emission of water vapour goes on entirely through the stomata. In very young leaves, before the cuticle has been fully formed, the surface of the epidermis itself can give off vapour; but in mature functional leaves the cuticle is quite impermeable to the vapour, and the stomata are the only means for its exit. The stomata, therefore, by their opening and closing, can regulate the transpiration of the plant. Generally speaking, they open in light and close in darkness, *i.e.* they open when the conditions are favourable for assimilation. Thus transpiration and assimilation go on together, an arrangement which is evidently highly expedient, for the current set up by transpiration brings to the leaves the water and mineral matter without which assimilation cannot take place.

A few words must be said as to the mechanism of the stomata, though the subject is too difficult to be discussed fully here. As a general rule, the stomata open when the guard-cells are turgid, and close when they are flaccid. This can be proved simply enough in the case of large stomata, such as we find in many Monocotyledons. A piece of epidermis is removed from a living leaf and mounted under the microscope, first of all in distilled water. The guard-cells curve more and more, and the pore between them opens to its full extent (see Fig. 95, *B*); next we replace the water by a solution of salt—a strength of 2 per cent. is sufficient. The curvature of the guard-cells now diminishes, and as they straighten themselves the pore between them closes (see Fig. 95, *A*). Now, how

are we to explain this? The pure water is absorbed into the guard-cells by the denser cell-sap, and so their turgidity is increased; conversely, the comparatively dense salt solution withdraws water from the guard-cells, and so they tend to collapse. But why do the guard-cells become more curved as their turgidity increases? This is mainly due to the ridges by which the wall of each cell is strengthened on the side towards the pore. This side of the cell is more rigid than the other, and so offers more resistance to stretching when water is taken up. Hence the more turgid the guard-cells become, the more do their outer walls stretch as compared with their inner walls, and hence the cells become more and more convex towards the exterior, and concave towards the pore. When water is withdrawn from the cells, just the reverse happens; the outer walls shorten more than the inner, and so the guard-cells tend to become straight and to close the pore between them. The mechanism of the stomata is in reality much more complex than appears from the above account, but the changes described are among the most important of those which bring about

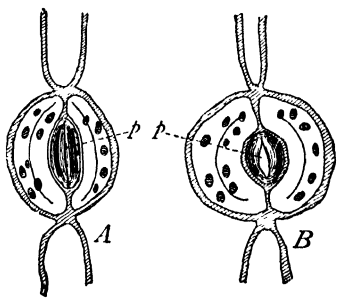


FIG. 95.—Stoma of *Amaryllis*. *p*, pore. *A*, In 2 per cent. salt solution; the guard-cells are flaccid, and the pore closed. *B*, In distilled water; the guard-cells are turgid, and the pore wide open. Magnified about 150 diameters. (R. S.)

the opening and closing of these organs. We have learnt, then, this much: the stomata open in light, and they open when the guard-cells are turgid. Can we, however, explain why the guard-cells become turgid in light? Although the exact significance of the chlorophyll granules in the guard-cells is unknown, it has been shown that, in light, the starch in the guard-cells is transformed into sugar, thereby increasing their turgidity and causing the stomata to open. In darkness, on the other hand, some of the sugar in the guard-cells is converted into starch, thereby decreasing the turgidity and causing the stomata to close.

The aqueous vapour transpired by the stomata comes immediately from the intercellular spaces, into which it has been given out by the mesophyll-cells, especially those of the spongy parenchyma. As transpiration goes on, the cells of the mesophyll constantly tend to become poorer in water, and they make good their loss by taking up fresh supplies from the water-conducting tracheids of the vascular bundles, by which every part of the leaf is traversed. We see now how appropriate is the comparison which has been drawn between the network of bundles in the leaf and the system of irrigation channels in a water meadow.

The rate at which water vapour passes out through a stoma depends upon the difference between the relative concentrations of water vapour outside and inside the stoma. When this difference is great, transpiration is rapid. Transpiration will tend to be greater with the air relatively dry. The removal of water vapour from outside a stoma by diffusion is a relatively

slow process. The removal, however, is quickened by bodily movement of the air, and hence transpiration is increased by wind. Increase of transpiration consequent upon increase of wind velocity and decrease in atmospheric humidity often results in the guard cells losing their turgidity, with the consequence that the stomata close. The transpiration may thus become even less than before. In some plants the loss of water by transpiration may be so great that the shoots wilt.

When transpiration is active, many of the tracheæ [1] become comparatively empty, the water forming a series of columns, the spaces between which only contain water vapour and an extremely small quantity of air, so that the pressure is very much below that of the atmosphere, and often becomes so reduced that we may speak of it as an approximate vacuum. From this fact alone it is quite evident that the pressure from the root does not keep pace with the transpiration from the leaves. If an actively transpiring plant be cut off just above the ground and placed with its cut end in water, the amount which its leaves give off as vapour may be more than ten times as much as that which is pumped up from the stump by root-pressure during the same time.

That the water ascends the stem through the wood can be well shown in any dicotyledonous tree in which the wood forms a continuous ring. Indeed, the experiment might be quite well carried out on our dicotyledonous type, the Wallflower, but a larger woody plant is more convenient for the purpose. A ring of tissue is removed from the stem, the part stripped off

[1] A term used to include both vessels and tracheids.

reaching inwards as far as the cambium, so that the whole of the cortex and phloëm are taken away. The wound is covered up with damp cotton-wool, or protected in some other way against evaporation. No withering of the leaves takes place, they remain indefinitely fresh and turgid as before; and if we measure the transpiration, the amount of water vapour given off is found to be undiminished. Hence it is evident that the current of water goes up just as well when the phloëm and cortex are interrupted as it does when they are complete. Only the wood and pith remain for it to pass through. It makes no difference to the result of our experiment if, as is usually the case, the pith is completely dried up and quite incapable of conducting water. Hence we can only conclude that the whole ascending current of sap passes through the wood.

In many trees, as for example the Beech, the whole thickness of wood continues to conduct water, even in trees more than a hundred years old. In others, as in the Oak, it is only the outer layers, forming the *sap-wood* or *alburnum*, by which water is conducted. In the latter case, if we repeat our ringing experiment, but make a deeper incision than before, so as to remove the outer, more lightly-coloured wood, as well as the phloëm, we get quite a different result. The leaves wither and dry up, and after a time all transpiration ceases; the water supply has evidently been cut off from the part of the tree above the incision.

Experiments in which plants are made to absorb coloured fluids have proved that it is through the vessels and tracheids of the wood that the water

ascends; the fibres take no part in the process. Whether the living cells of the woody parenchyma and of the medullary rays do or do not help in the conduction of water is still an open question.

As to the *causes* of the ascent of water in the wood, we are still very much in the dark. The pressure in the living cells of the root, no doubt, has much to do with the forcing of water into the vessels in the first instance. The constant giving-off of water vapour by the transpiring leaves is also of great importance, for it causes a pull on the water in the vessels below. The extremely low pressure in the vessels and tracheids must help the movement of the columns of water which they contain, and this movement will tend to be in the right direction, for it has been proved that the pressure becomes still less as we approach the leaves than it is in the lower parts of the stem.

Certain physical forces can be eliminated as affording an explanation of the rise of the transpiration current. Atmospheric pressure will only maintain water to a height of about 33 feet. We know that some trees are about 300 feet high, and yet their topmost branches suffer no lack of water. Capillary action, by which water rises in narrow tubes, will not account for maintaining sap in the vessels and tracheids, for these natural tubes are not nearly narrow enough to maintain water to anything like the height required. Thus, in a tube $\frac{1}{500}$ inch in diameter, which would be rather small for a wood-vessel, water will only rise by capillarity to a height of about two feet.

A very tempting explanation, which many botanists have adopted, is to suppose that the living cells of the wood take part in the work, absorbing water from the vessels, and pumping it out again under pressure, just as we know takes place in the case of the living cells of the root. As in certain cases, however, experiments appear to show that the sap will continue to rise in stems more than 33 feet high, which have been completely killed, this explanation is open to much doubt.

It has, however, been shown recently that a column of water will bear a considerable tensile stress without rupture. Many botanists now think that, in conjunction with the forces available in the root and the pull exercised by transpiration from the leaves, the tensile strength of the water columns in the tracheæ is sufficient to account for the ascent of sap to the tops of the tallest trees.

V. *Respiration.*—We will now leave the subject of nutrition, and say something about a chemical process of quite another kind, by which the plant instead of gaining substance loses it, but in doing so gains energy for the work which it has to perform. This process is the *breathing* or *respiration* of plants. So long as plants are in active life, the great majority of them, like animals, are continually taking up oxygen from the air, and giving off a corresponding amount of carbon dioxide. The latter, as we know, is a product of combustion. The oxygen which is absorbed is taken up by the protoplasm, and ultimately combines with a portion of its carbon. The product of oxidation, carbon dioxide,

is given off again into the air. The breathing of plants is, in fact, just the same thing as our own breathing, or that of other animals. We must be very careful not to confuse respiration with carbon-assimilation. In both processes an exchange of gases between the plant and the atmosphere goes on. In assimilation, however, the plant gains carbon at the expense of the carbon dioxide of the air, while in respiration it loses carbon at the expense of its own carbon compounds. The former is a constructive process, by which more complex bodies are built up out of simpler ones; the latter is a destructive process, by which complex substances are broken down into simpler ones. In assimilation deoxidation takes place, while respiration is a process of combustion or oxidation.

In the case of green organs exposed to light, the two processes go on together. In light of ordinary intensity assimilation is much more vigorous than respiration, so that carbon dioxide is decomposed much more quickly than it is formed. In darkness, however, assimilation ceases, and then it is easy to prove that carbon dioxide is given off. The same is the case, whether in light or darkness, with any organs which are not green, such as flower-buds or seeds just beginning to germinate. In order to prove that carbon dioxide is evolved, a number of seeds are allowed to germinate under a bell-glass, which is fitted with tubes through which a current of air can be drawn. The air which enters the apparatus is deprived of all its carbon dioxide by passing through a solution of caustic potash. The same air, after it has passed over

the seeds, is drawn through lime water, in which it throws down a precipitate, owing to the formation of calcium carbonate ($CaCO_3$). By drying and weighing the precipitate, we can tell how much carbon dioxide has been formed by the germinating seeds in a given time.

As a rule, subject, however, to many exceptions, the volume of carbon dioxide given off in respiration is about equal to that of the oxygen taken in. Organs which are altogether deprived of oxygen can, however, go on breathing for some time. This is called *internal* or *intramolecular*, as distinguished from *normal*, respiration. It is probable that in both kinds of respiration the oxygen as well as the carbon is derived from the protoplasm itself. In normal respiration, however, the loss of oxygen is made good by fresh supplies from the atmosphere. In intramolecular respiration, where this is not the case, the process can only go on for a limited time in most plants.

It cannot be too strongly insisted upon that all parts of plants breathe at all times so long as they are in active life. It is only when the protoplasm is completely at rest, as in a dry seed or bulb, that, respiration ceases. If respiration is stopped, all the work of the plant is stopped also; all the chemical changes in the plant come to an end; growth ceases, and so do the protoplasmic movements, such as we studied in *Elodea*. Just as the combustion of the coals in the fire-box of a steam-engine supplies the energy for the work of the engine, so does the combustion of carbon in the plant's protoplasm supply energy for the

growth of the plant, and for such movements as it performs. The plant, in fact, like an animal, must breathe in order to live, but as in most cases the plant does not have to execute such active movements as an animal, the actual amount of oxygen which it has to consume is so much less.

Respiration being a form of combustion, heat must of necessity be set free. As a rule, however, no consequent rise of temperature is observed in the case of plants; for the plant in most cases loses heat more rapidly than it gains it. An ordinary leafy plant has an enormous surface in comparison with its bulk, and is thus exposed to very rapid cooling, both by radiation and conduction. The vaporisation of water during transpiration also uses up more heat than respiration can supply. It is only when actively breathing organs are crowded closely together in a confined space that a rise of temperature can be detected. If the bulb of a thermometer be thrust into the midst of germinating seeds, a temperature about 1·5° C. higher than that of the surrounding air may be observed, and in some plants with very crowded flower-buds, enclosed in a sheathing bract, a much greater rise of temperature takes place in consequence of respiration (as in *Arum*).

VI. Growth.—By growth, increase in size is usually meant. This generally involves increase in weight, although a seedling growing in darkness may actually lose weight notwithstanding the increase of the young plant in length. Normal plant growth, however, involves an increase of both size and weight.

In plant as in animal growth the protoplasm increases

in amount, and one of the most remarkable properties of life is the enormous increase of protoplasm during the development of the seed into the adult plant. An oak tree, for instance, contains many thousand times as much protoplasm as the acorn from which it sprang. All this growth in the protoplasm arises from the intake into the protoplasm of the acorn of simple food substances from the soil and air, and the elaboration of these into additional protoplasm.

It has been explained in earlier chapters of this book that growth in flowering plants takes place by means of *meristems* or groups of actively dividing cells. These meristems are confined to the apical regions in most monocotyledonous stems and roots, but in Dicotyledons there are additional meristems, viz. the cambium and the phellogen (or cork cambium), both in stem and root. Any cell which retains its protoplasm is potentially capable of division, but resumption of meristematic activity in highly vacuolated cells is exceptional apart from the development of the interfasicular cambium and the phellogen in Dicotyledons.

Growth in length of the stems and roots of flowering plants involves two distinct processes. In the first place the apical meristems give rise to new cells. These also divide for a time, but most of them, even in Dicotyledons, then cease to divide. At this period vacuoles appear in the cytoplasm, and many of the cells become greatly distended, especially in a longitudinal direction. This elongation of cells no longer dividing is responsible for a large part of the increase in length of stems and roots. In the process of ex-

tension each cell at first elongates slowly, then more rapidly, and finally slowly again until it reaches its maximum length. As might be expected from the position of the elongating cells, the region of maximum elongation in stems and roots is not exactly at the apex of the stem or root, but a short distance behind it. If, for instance, the radicle of a germinating Broad Bean, when about an inch long, is marked from the apex backwards with rings of Indian ink at intervals of $\frac{1}{10}$ of an inch, and is then allowed to grow vertically downwards in a moist atmosphere, it will be found after a short time (twenty-four hours) that the rings of Indian ink are now unequally spaced. The apical zone will be slightly longer than $\frac{1}{10}$ of an inch, the second zone (from the apex) will have elongated most, the third zone will have elongated much less than the second zone, the fourth zone will have elongated only very slightly, and the fifth and subsequent zones will have elongated not at all.

Like all other physiological processes the rate of growth is dependent upon such external conditions as temperature and light, and upon certain internal conditions such as the age and degree of turgor of the cells. Other things being the same, a plant grows more rapidly the higher the temperature up to a certain point, beyond which the rate of growth decreases. In most plant stems the rate of elongation is greater in darkness than in light. The rate of elongation of a developing stem, *e.g.* that of a sunflower, is not uniform throughout the whole period of development: at first the rate of elongation is small, then it increases to a maximum, after which it becomes slower again, and finally ceases

as the plant reaches its full height. In this respect the elongation of the whole shoot is comparable with that of the individual cell.

VII. Movement of Plant Organs.—It is commonly supposed that one of the chief differences between plants and animals is that the former remain fixed in one position while the latter move freely. This belief is not strictly true, for, as will be seen in Part II. of this book, some of the lower plants move as freely as the simplest types of animals. Even in the flowering plants many of the organs are capable of movement in response to the action of gravity, light, etc., although the plants as a whole remain in a constant position.

Let us first consider the movements of the shoot and root of a flowering plant in relation to gravity. A convenient plant for our purpose is the Broad Bean (*Vicia faba*). It is a matter of common observation that, under normal conditions and even in darkness, the young shoot grows vertically upwards and the radicle downwards.

If, when the plant is in darkness, these organs be displaced out of their vertical position, their extremities will tend to revert to the vertical within a short time. If, for instance, a seedling bean with a radicle about an inch long be placed with the radicle horizontal under moist conditions, so that growth can be continued, the portion of the young root near the tip will begin to bend downwards within twenty-four hours. In forty-eight hours the extremity of the root will be pointing directly downwards, while the rest of the root will be still horizontal. The region of curvature is a short distance

behind the tip of the root, and it will be found that the position of curvature coincides with the region of greatest elongation, as described on p. 235. The downward movement of the extremity of the root occurs in response to the influence of gravity, and the radicle is said to be positively *geotropic*. The extremity of the root is similarly responsive to certain other forces, *e.g.* centrifugal force. If a germinating bean is placed on a wheel which is revolved rapidly in a vertical plane so that the radicle lies at right angles *across* a radius, the extremity of the root after a short time will be found to have curved so that the tip is directed outwards *along* a radius. It can be shown that the direction assumed by the tip of the root on the revolving wheel is independent of the exact magnitude of the centrifugal force. The curvature of the root apex in this experiment is said to be a response to the *stimulus* of the centrifugal force. In the same way the downward curvature of the tip of a bean radicle placed horizontally is said to be a response to the stimulus of gravity. Curvatures arising in response to stimuli are called *tropisms*.

It can be shown that the part of the root which perceives the stimulus of gravity is not the same as that which responds. If the root tip of a similar bean seedling is carefully [1] cut off with a sharp razor and the radicle laid horizontally, no downward curvature will take place. This suggests that the root tip is the region which perceives the stimulus of gravity.

[1] Unless great care is taken, abnormal curvatures arise which may take any direction and which are attributed to injury.

Many suggestions have been made as to the exact manner in which the influence of gravity is perceived by the root tip, and how this influence is transmitted to the region where the response occurs, but we are still very much in the dark as to the real explanation of this remarkable reaction.

The secondary roots which arise from the radicle or primary root at a later stage are not responsive to gravity in quite the same way, for they take up a position directed obliquely downwards at a more or less constant angle with the primary root. If, however, the latter is injured and thereby rendered incapable of responding to gravity, one or more of the secondary roots behave in the same way to gravity, *i.e.* grow vertically downwards, as the primary root normally does.

In contrast to the behaviour of the radicle the plumular shoot of a bean seedling, upon being placed in a horizontal position in the dark, will respond to the stimulus of gravity within a short time by its extremity assuming the vertical position. This change is effected by a curvature of the stem at some little distance behind the apex. The plumular shoot is said to be *negatively geotropic*. All young growing stems, which normally grow erectly, are likewise capable of reassuming the vertical position if displaced from it.[1] Lateral branches, even when in the dark, grow out more or less horizontally from the main stem, and are said to be *diageotropic*; but if the upper part of the main stem is destroyed, one or more of the lateral branches begin

[1] In grasses and cereals the curvature is effected at the lower part of one of the lower nodes, a large portion of the stem becoming erect.

to grow erectly in response to gravity, to replace the lost "leader."

The reactions of plant organs to the stimulus of light are no less striking. Every one has seen the young stems of plants on a window-sill bending towards the window. The young stem is said to be *positively phototropic*, and bends from the side where the light intensity is weaker towards the side where it is stronger. In nature the light is usually equally strong on all sides so that the main shoots grow vertically upwards. It is only the young part of the stem, still capable of elongation, that is able to respond phototropically. Greater growth occurs on the side exposed to the relatively weak light intensity (*i.e.* the side remote from the source of illumination) as compared with the growth on the side facing the stronger light intensity.

With most young roots, however, light does not affect the rate of growth, and the direction of growth is unaffected by different light intensities on opposite sides. The primary root of a mustard seedling is an exception to this general rule, as it is markedly *negatively phototropic*. Leaves are generally arranged so that the brightest incident light is perpendicular to the surface; they are said to be *diaphototropic*. If the direction of the light be changed, the petiole twists or bends so that the lamina is orientated into a position with the new direction of the light perpendicular to the surface.

There are several other external factors to which plant organs respond. Another potent influence which may

direct the growth of a young root is a difference of humidity on the two sides, the extremity always bending towards the region of greater humidity. The young parts of roots are said to be *hydrotropic*. The influence of differences of humidity may be so great as to overcome the influence exercised by gravity. If, for instance, barley seeds are placed upon a sieve with narrow meshes, suspended obliquely in the air, and the sieve is kept moist, the radicles will at first grow vertically down through the meshes, but will soon bend towards the surface of the sieve because of the greater humidity on the side of the root towards the sieve than on the side away from it.

Movements of tendrils may be induced by the stimulus of contact with the solid objects around which they eventually curl. The leaflets of the Sensitive Plant (*Mimosa pudica*) fall down when touched, the stimulus being transmitted along the rachis so that the leaflets fall successively. A change of position of the leaflets of the Sensitive Plant and some others (*e.g.* clover) occurs at nightfall. As is well known, many flowers, *e.g.* tulip, close at night, the response here being due to a fall in temperature. In some cases leaflets undergo continuous movement without change in external conditions. In clover this diurnal movement is very slow, but it can be observed if a long, light pointer is attached to a leaflet.

Before leaving this subject it may be pointed out that the response of plant organs to external stimuli is generally advantageous to the plant. The upward growth of the plumular shoot in response to gravity

brings it into the light, where its direction of growth may be changed phototropically if the light intensity is not uniform on all sides. The downward movement of the radicle in response to gravity and its orientation towards the region of greater humidity are both of supreme significance in relation to the primary functions of roots.

Under exceptional conditions the plant still responds in the normal manner, which under these particular conditions is actually disadvantageous. If, for instance, a seed be placed near the bottom of a flower-pot and covered with soil, upon germination the plumule will still grow upwards through the soil and may actually exhaust itself before reaching the surface, whereas if it had grown downwards through the hole at the bottom of the pot it would soon have reached the light. The exact manner in which such movements as those described above have been brought about in the course of evolution is very obscure and beyond the scope of this book to discuss.

CHAPTER IV

TYPE III

THE SPRUCE FIR (*Picea excelsa*, Link.)

I. *EXTERNAL CHARACTERS*

THE Spruce, a type which will be well known to all readers, is a coniferous forest tree, sometimes reaching as much as 150 feet in height. It is not a native of Britain, though frequently planted. Small specimens of this Fir are those generally used as our Christmas trees. In Northern Europe and in the mountainous districts of Central Europe the Spruce forms large woods, and extends almost to the extreme limits within which trees can grow. In the North it reaches Lapland and Arctic Russia, while on the Alps it is found up to a level of more than 6000 feet.

The tree has a pyramidal form; its main stem is straight and vertical. The principal branches grow out from it almost horizontally or slope slightly downwards; the smaller twigs are nearly upright.

The leaves are spirally arranged and crowded together. They are needle-shaped, and are bluntly four-cornered in transverse section. Each leaf is traversed from end to end by a single vein (see Figs. 96 and 101).

The branches arise in the axils of the leaves, but only a very small proportion of the axillary buds are ever developed.

The root-system consists entirely of the tap-root and its numerous ramifications. Both stem and root, like those of Dicotyledons, grow in thickness from year to year. Hence the main stem and its branches have a somewhat conical form, for they are thickest at the base and taper gradually towards the apex. The older parts of the stem are covered by a scaly bark, which peels off in thin flakes.

The tree is evergreen—that is, it does not shed all its leaves in any one season ; the same leaves remain upon it for about three years, and new leafy shoots appear each year, so that the tree is never bare.

The young shoots, which will expand in the following year, pass the winter in the form of buds, which are enclosed within the *bud-scales* ; these are modified leaves of a light brown colour, and thin membranous texture.

As with all other types of trees the Spruce does not bear reproductive organs until it is several years old. The Spruce, like most, though not all of the cone-bearing trees, is *monœcious*,[1] *i.e.* the cones are of distinct sexes but are both borne on the same plant. They are extremely different from the flowers which we have considered hitherto, and indeed bear little resemblance to the flowers of any of the Angiosperms. One peculiarity which is common to the cones of both sexes, is that the floral axis is elongated and bears spirally-arranged leaves, so far resembling an ordinary vegetative branch, whereas in typical angiospermous flowers the axis is shortened, and the floral leaves

[1] A flower, like that of the Wallflower or Lily, which contains both stamens and pistil, is called *hermaphrodite.*

are therefore brought close together at nearly the same level.

The male cones of the Spruce are borne in the axils of the leaves of a shoot formed in the previous year (see Figs. 96, *B*, and 110, A). The cone or *strobilus* begins with a short stalk, on which are borne some bright green

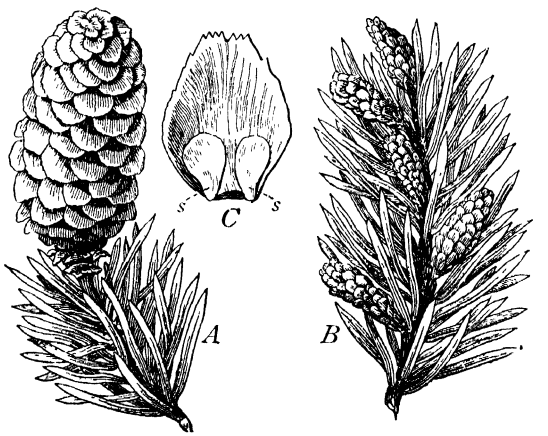


Fig. 96.—*A*, Twig of *Picea excelsa*, bearing a young female cone. *B*, Twig bearing several male cones. *C*, Seminiferous scale from the female cone of *A*, showing two winged ovules on the upper surface. *A* and *B* slightly reduced, *C* enlarged. (After Beissner.)

bracteoles. There is no perianth; above the bracteoles the axis only bears the stamens, which are numerous and arranged in a spiral. The leaf-like stamens are of a bright red colour; in each of them the free end of the staminal leaf is bent upwards at an angle with the horizontal stalk. On its lower surface the stamen bears two pollen-sacs, lying side by side,

parallèl to the stalk (see Fig. 110, p. 266). The details of the pollen-sacs and pollen will be described later.

The female strobili or cones grow at the ends of last year's twigs (see Fig. 96, *A*). At the end of May, when the cones open, they are from 1½ to 2 inches in length and of a beautiful red colour. At this time they are erect; later on they become pendulous. The cone consists of a central axis, bearing crowded spirally-arranged scales. Each scale is of an obovate form (see Fig. 96, *C*), often with a blunt point at the end. The scales are not themselves the carpellary leaves, though they have all the appearance of foliar organs. More careful examination, however, shows that each scale stands immediately above a small narrow pointed leaf, which may be regarded as corresponding to a carpel. Except in the youngest stages these little leaves are very inconspicuous compared with the scales, but they are developed before them, and in fact each scale arises at first as an outgrowth from the upper surface of the carpellary leaf and close to its base. The scales soon outgrow the leaves which produce them, and by the time the flower opens they alone can be seen from outside, the carpels being quite buried between them.

Each scale bears on its upper surface and near its base two ovules, with their micropyles directed inwards towards the axis of the cone. Each ovule is attached to a flat wing, much larger than itself, which is formed from the upper surface of the scale (see Fig. 96, *C*).

When the female cone matures, after its ovules have been fertilised, it undergoes but little change compared with an angiospermous flower when it becomes a fruit. The

whole cone grows much larger, attaining a length of from four to six inches. The scales first turn green and then brown, growing hard and woody, and the ovules, as they ripen into seeds, acquire a hard testa. Their wings remain attached to them, and become dry and membranous. The scales of the cone close firmly together, shutting in the seeds. We thus see that all the parts which constituted the young cone are still present at maturity, which is not often the case with the angiospermous flower and fruit.

The seeds are ripened in the autumn after flowering, but it is only in the following spring that the scales of the cone open out and the seeds fall. The wing to which each seed is attached offers a broad surface to the air, and so enables the seeds to be scattered more widely by the wind.

The most striking point in the whole history of the female cone, as compared with the flower of an Angiosperm, is that there is no closed ovary at the time of pollination. When this process takes place, the scales are separated from one another sufficiently to leave an open passage down to the ovules, and it is upon the micropyle of the ovule itself that the pollen falls. There is thus no need for a stigma and a style. On this character, which is common to the whole Class of cone-bearing trees and their allies, the name *Gymnosperms*, or plants with naked seeds, is based.

It is only after pollination that the scales close up so as to shelter the developing seeds, opening again when the latter are ripe, and so allowing them to escape. The gymnospermous structure is an obvious difference from other Flowering plants, and will prepare us for

the still greater differences which we shall find when we come to consider the development in detail.

Having now given a brief sketch of the chief points in the external morphology of our type, we will go on to examine its more minute structure.

II. *ANATOMY OF THE VEGETATIVE ORGANS*

a. Stem

The structure of the young stem in its main features is closely similar to that of a normal Dicotyledon (see Fig. 97).

The central cylinder contains a single ring of vascular bundles enclosing a pith. The bundles themselves, just as in Dicotyledons, are collateral, with their xylem directed towards the centre, and their phloëm towards the exterior of the cylinder. These bundles pass out one by one into the leaves, each of which receives a single bundle only (see Fig. 97, *l*). The bundles in the cylinder are separated from one another by the primary rays, which are only two or three cells in thickness.

The primary bundles are of simple structure. The xylem consists entirely of tracheids and parenchyma; no vessels are developed at any time in the wood, whether primary or secondary, of the Fir or any other cone-bearing trees. The protoxylem, which lies at the extreme inner side of the bundle, has the usual spiral or annular tracheids; the phloëm consists of sieve-tubes and parenchyma. There are no companion-cells, but certain cells of the parenchyma bordering on the

sieve-tubes are richer in protein materials than the rest, and may discharge the function of companion-cells.

Between xylem and phloëm we find a layer of actively dividing cambium, just as in the vascular bundle of a Dicotyledon. Later on, too, divisions take place in

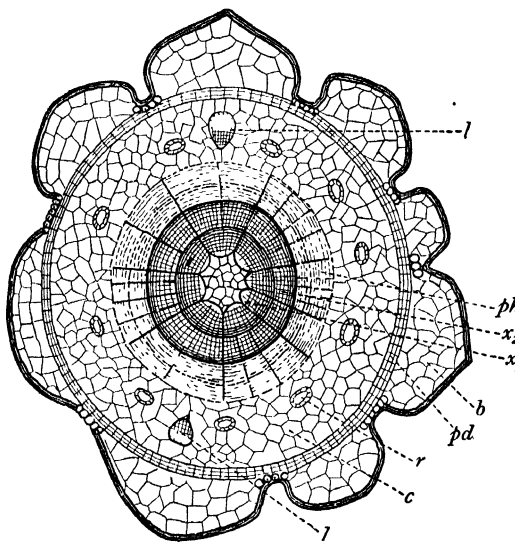


FIG. 97.— Semi-diagrammatic transverse section of a two-year-old stem of *Picea excelsa*. *b*, base of leaf; *pd*, periderm; *c*, cortex; *r*, resin canal; *ph*, phloem; x_2, second year's wood; x_1, first year's wood; *l*, leaf-trace bundle. Magnified about 40. (R. S.)

the medullary rays, so as to form an interfascicular cambium which completes the ring. Fig. 97 shows a transverse section of a twig of the second year, when a good deal of secondary tissue has already been formed. The cambium acts precisely in the same

way as in a Dicotyledon, and needs no special description.

The cortical tissue is chiefly remarkable because it contains a ring of *resin canals* (*r* in Fig. 97). The resin canal is an intercellular space, surrounded by a circle of thin-walled cells rich in protoplasm; these cells secrete the resin, which is poured into the canal. The canal itself arises by the splitting apart of a group of cells so as to leave a space between them. The canals extend for long distances through the stem. The secreting cells lining the cavity are called the *epithelium* of the canal. The epithelium is surrounded by another ring of cells, which have rather thicker walls than those of the cortex generally. The resin may be of use to the plant by rendering it distasteful to animals, which might otherwise attack the young twigs; it probably has other functions also. Resin-canals are also present in the wood and medullary rays. They are by no means peculiar to Gymnosperms, occurring, for example, in the Ivy.

The outline of the young stem, as shown in Fig. 97 in transverse section, is rendered irregular by the projecting bases of the leaves. The older branches, however, are cylindrical. This change is due to the formation of *periderm*, which arises, as in the Wallflower, from a *phellogen* or cork cambium, but in the Fir the phellogen is formed by the division of a ring of cortical cells, not from the pericycle. Opposite the depressions between the leaf-bases the phellogen arises quite near the surface, but opposite the leaf-bases themselves it is deeply seated, and thus the whole layer is nearly circular, as seen in transverse section (see *pd* in Fig. 97). Cork is formed by the phellogen towards the exterior, and everything out-

side the layer of cork dries up, and is cast off. Thus the irregularities of the surface are removed, and the new surface formed by the cork is smooth and cylindrical. Later on, however, new layers of phellogen arise, by the division of deeper cortical layers, and so a scaly bark is formed, such as we find on the older stem or branches. The bark, as we know, consists of the cork, together with all the dried-up tissue outside it.

We will now go on at once to describe the changes which take place in the twig when it becomes a thick branch or trunk. After what we have already learned of the development of the Wallflower, it is quite easy to understand this process, though the change from a little twig, $\frac{1}{16}$ of an inch thick, to the stem of a great Fir-tree a yard or more in diameter, is certainly a remarkable one.

We have seen that there is always a layer of cambium between the wood and bast of each bundle, and that by the divisions of the interfascicular tissue the cambium becomes united into a complete ring. When the cambial cells divide, they cut off cells on the inner side, which after one or more further divisions become elements of the wood. In like manner the cells cut off from the cambium on its outer side, after subdividing, become part of the phloëm. Hence, just as in the Wallflower, the oldest part of the wood is always that nearest the pith, while the oldest part of the bast is that nearest the cortex. The most recently formed part of each is found near the middle of the secondary zone next the cambium.

The secondary wood is of simple structure compared with that of most Dicotyledons. It consists entirely of tracheids and medullary rays; there are no vessels, and there is no woody parenchyma, but the wood is traversed by resin canals, which have their secretory

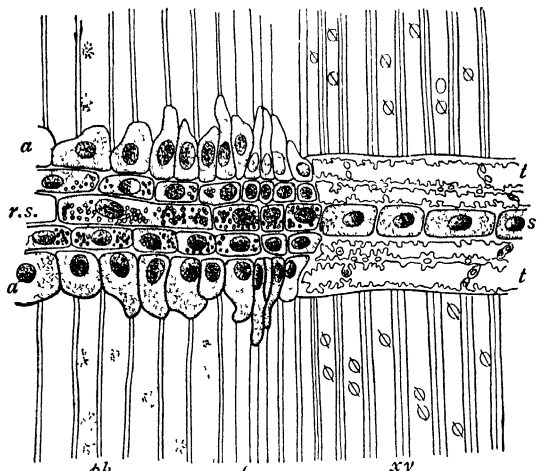


FIG. 98 — Radial section of the wood and bast of the Scotch Fir (*Pinus sylvestris*). *xy*, xylem; *c*, cambium; *ph*, phloem; *a*, *r.s*, *a* to *t*, *s*, *t*, medullary ray; *t*, *t*, tracheids of ray; *s*, starch-containing cells; *a*, *a*, albuminous cells; *r.s*, starch-containing cells. Magnified. (After Strasburger.)

epithelium. The tracheids are long, pointed elements, reaching a length of from two to four millimetres; they are as a rule pitted on their radial walls only.

The pits are of the *bordered* kind, and afford the best examples of this structure. On each radial wall of the tracheid there is a single row of large bordered

pits. Their construction is shown in Fig. 99. Seen in surface view, *i.e.* in a *radial* section through the wood, each pit appears as two concentric circles (Fig. 99, *A*). The meaning of the two circles only becomes clear when we examine a pit in sectional view, such as we see in either a tangential (*B*) or a transverse (*C*) section of the wood. We now find that the pit, like all other pits, is essentially a thin place in the cell-wall. The thin part of the wall or *closing membrane* is over-arched on both sides by a circular rim, which projects over it so as to leave only a narrow opening in the middle of the rim. The closing membrane itself is not of equal thickness all over, but has a thicker part in the middle, called a *torus* (*t* in Fig. 99, *B* and *C*). We now see that in the surface view (*A*) the outer circle corresponds to the external edge of the projecting border, while the little circle in the middle is the opening in the border leading to the closing membrane. The structure of all bordered pits is similar, but they are most easily studied in plants of the Fir kind on account of their large size.

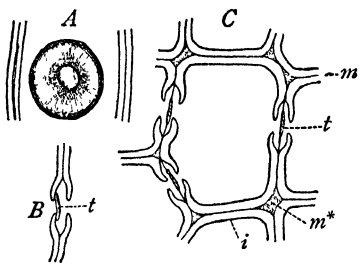


FIG. 99.—Bordered pits of a Fir. *A*, Part of tracheid with pit in radial view. *B*, Pit in tangential section: *t*, torus. *C*, Transverse section of tracheid, showing pits: *t*, torus; *m*, middle lamella; *i*, inner layer of cell-wall. Magnified about 400. (After Strasburger.)

We must remember that the tracheids are closed

cells, so that no communication is possible between them except through their pits. The whole of the water which goes up a Fir-tree has to pass through the bordered pits thousands of times on its journey from the roots to the leaves. The thin membrane is protected from rupture by the torus. When the pressure is much higher in one tracheide than in its neighbour, the closing membrane is bulged out, becoming convex on the side towards the lower pressure. Thus the torus is pressed closely against the opening of the pit border on that side (Fig. 99, *B*). The thin part of the membrane is thus supported by the border, and only the thickened torus is exposed to the full pressure.

The border has another important function; it serves to keep the closing membrane moist. In times when transpiration is very active, and the water-supply deficient, as in hot, dry summers, the tracheids become very nearly emptied of water. Within the minute cavities of the bordered pits, however, the water is held fast by capillary action, and so the closing membranes are prevented from drying up. Thus the entrance of air into the tracheids is guarded against.

The wood is not uniform all through. As everybody has seen, the wood of the Fir, like that of other trees in temperate climates, shows *annual rings*, each ring representing a year's growth, so that by counting them the age of the tree can be ascertained.

The reason why we can detect the annual rings is that the wood formed in autumn has a different

structure from that developed in spring. Thus there is a sharp boundary between the autumn wood of one year and the spring wood of the next. This difference in the case of the Fir-tree is due to the fact that in the autumn wood the tracheids are much narrower radially and have much thicker walls than those formed in spring (see Fig. 100). The last-formed

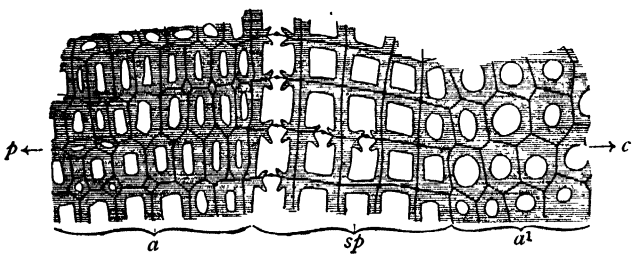


FIG. 100.—Portion of transverse section through the wood of *Picea excelsa*, showing spring and autumn wood. The arrow *c* points towards the cambium, the arrow *p* towards the pith ; *a*, autumn wood ; *sp*, spring wood ; a^1, beginning of autumn wood of second year. Magnified 330. (R. S.)

layers of the autumn wood, unlike all others, have pits on their tangential as well as on their radial walls. Through these tangential pits the water passes to the cambium, and to the spring wood as soon as it is formed in the following year.

The *medullary rays* vary very much in size. Many of the rays are only one cell thick, and some of these may be only one or two cells in height ; others are several cells in thickness, and proportionately higher.

The elements of which the rays are composed are of two kinds. Some are living parenchymatous cells in which starch is formed (see Fig. 98, *s*). Others, however, completely lose their living contents, and become tracheids (see Fig. 98, *t*, *t*). These have bordered pits like the long tracheids of the wood, and their walls are irregularly thickened. These tracheids in the ray serve for the passage of water in the radial direction, so that by their help communication is kept up between the different layers of the wood. The parenchymatous ray-cells have only simple pits, except where they are in contact with tracheids, in which case the pits are bordered on the side towards the tracheid. The parenchymatous cells serve for the storage of reserve food-substances, especially starch and oil. The two kinds of elements in the ray are arranged in horizontal rows. Often we find rows of tracheids at the top and bottom of the ray, and parenchymatous cells in the middle.

The resin canals which traverse the wood resemble those already described; their cavity is surrounded by a layer of thin-walled secreting cells. In each of the larger medullary rays a horizontal resin canal is usually found. These horizontal canals are in communication with the vertical ones.

Summing up the peculiarities of this example of coniferous wood, we find that its great characteristic as compared with the wood of a Dicotyledon is its less perfect differentiation. Vessels and woody fibres are both absent. The tracheids have to do duty for both, those of the spring wood taking the

chief part in conducting water, while the thick-walled autumnal tracheids serve mainly for strength. Ordinary wood-parenchyma is also absent, the only parenchyma, apart from the rays, being the secreting tissue of the resin canals. On the other hand, the rays themselves are more complex than those of most Dicotyledons. As the wood increases in thickness, new secondary rays are started by the cambium, just as we found in the Wallflower.

The secondary *phloëm* of the Fir is made up of *sieve-tubes*, variously modified *parenchyma*, and *phloëm rays* of complex structure. The sieve-tubes are long, pointed elements, resembling in form the tracheids of the wood. They have sieve-plates on their radial walls only (see Fig. 98, *ph*). The pores of the sieve-plates are excessively minute compared with those in Angiosperms. The sieve-tubes, as in other vascular plants, contain proteins, and probably help to transport them. The phloëm parenchyma forms tangential bands between the zones of sieve-tubes. Some of its cells contain starch or crystals of calcium-oxalate, while others become very thick-walled, forming the *stone-cells*.

The medullary rays in the phloëm consist of two kinds of cells: (1) ordinary parenchymatous cells which form starch (see Fig. 98, *r.s.*); (2) cells which are more elongated in the vertical direction, contain no starch, and are very rich in proteins (see Fig. 98, *a*, *a*). These cells (which are called the *albuminous* cells) communicate by pits with the sieve-tubes, and are believed to fulfil the same functions as the companion-cells of angiospermous sieve-tubes.

The phloëm ray is simply the outer part of the same medullary ray which passes through the xylem, and the cambium serves for the growth of both (see Fig. 98).

We see, then, that the portions of the medullary rays which pass through the phloem show a similar differentiation to that of the same rays in the wood. In both alike there are two kinds of elements, one kind serving for the storage of reserve materials, while the other forms part of the conducting system.

b. Leaf

The leaves of the Spruce and those of most Coniferæ differ greatly from the typical leaves of Dicotyledons. In our type they are very simple in structure, and the bundle-system especially is much reduced. As we have seen, a single vascular bundle enters each leaf from the stem. Sometimes this bundle divides into two, which run side by side through the leaf. In other cases, as in that figured, the bundles are united into one (see Fig. 101). The bundle forms part of a central cylinder which traverses the leaf from end to end, and is continuous with the tissues of the central cylinder of the stem. The cylinder of the leaf is surrounded by the mesophyll, which in this species shows no distinction between palisade and spongy parenchyma, though in some other Conifers this differentiation is present.

We will now consider the structure of a leaf more in detail. The form of the leaf as seen in transverse section is quadrangular. Its natural position is such

that the diagonals of the square are vertical and horizontal (see Fig. 101). The epidermis has a thick outer wall, which is cuticularised. The stomata are arranged in lines along each of the four flat surfaces of the leaf. The guard-cells are sunk below the surface, and are almost covered in above by two very thick-walled epidermal cells, so that scarcely anything

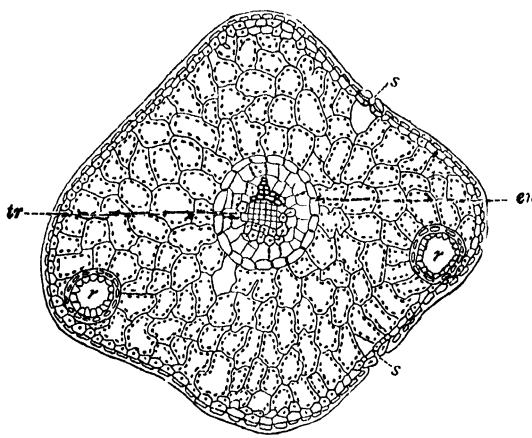


FIG. 101.—Transverse section of a leaf of *Picea excelsa*. *s*, stomata; *r*, resin canal. In the middle observe the central cylinder with a single vascular bundle, in which the xylem is directed upwards. *en*, endodermis; *tr*, transfusion tissue. Magnified 82. (R. S.)

can be seen of the stoma itself in a surface view of the leaf. In a transverse section (see Fig. 102) there appear to be two pairs of guard-cells, one above the other, but only the lower cells belong to the stoma, and they alone take part in the opening and closing of the pore. Beneath each stoma is a large intercellular air-cavity.

Next below the epidermis comes the *hypoderma*, a layer of cells which are elongated parallel to the axis of the leaf. They have extremely thick walls, and help much in giving rigidity to the whole organ. The hypodermal layer is interrupted below the stomata, while at the corners of the leaf it may be more than one cell thick.

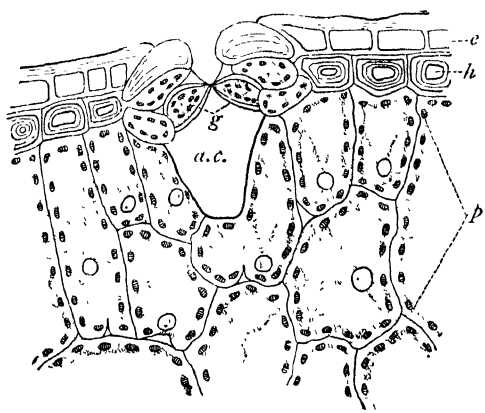


FIG. 102.—External tissues of leaf from the same section as Fig. 101; enlarged to show details. *g*, guard-cells of stoma; *a.c*, air-chamber; *e*, epidermis; *h*, hypoderma; *p*, assimilating parenchyma. Magnified 330. (R. S.)

Within the hypoderma we find the most important part of the leaf-tissue, namely, the assimilating parenchyma, containing chlorophyll granules. This forms a thick layer, and indeed makes up the greater part of the substance of the leaf. Its cells are thin-walled and rather irregular in shape, and their cell-walls are often somewhat folded. The cells contain in-

numerable chlorophyll granules, which are embedded in the protoplasm lining the cell-wall (see Fig. 102).

In the mesophyll we very often find two resin canals placed near the two lateral corners of the leaf (Fig. 101, *r*). The resin canals have the usual structure, namely, a layer of secreting epithelium next the cavity, and a strengthening ring of sclerenchyma surrounding the epithelium. These resin canals are not very constant in their occurrence. Sometimes there is only one, sometimes there are none at all. When present, the canals end blindly at the base of the leaf, so that they do not join on to those of the stem. This shows that the leaf forms its own resin and keeps it to itself.

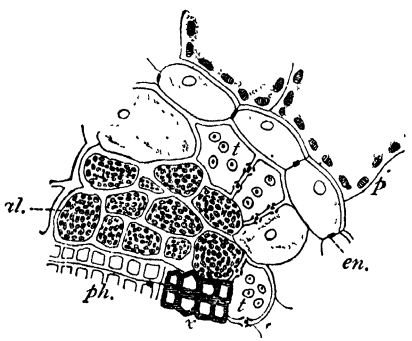


FIG. 103.—Part of the central cylinder and adjoining tissue of the leaf of *Picea excelsa*, in transverse section; from the same section as Fig. 101, more enlarged. *p*, cells of assimilating parenchyma; *en*, endodermis; *t*, transfusion tissue of cylinder; *al*, albuminous cells; *ph*, part of the phloëm of bundle; *x*, part of the xylem of bundle. Magnified 330. (R. S.)

We now come to the central cylinder. This is marked off from the mesophyll by a regular endodermis, which has essentially the same structure as the endodermis of a root (see Fig. 103, *en*). Within the endodermis we find the conjunctive tissue of the cylinder, and in the middle of this is the vascular bundle.

We will describe the latter first. It is generally a double bundle in the lower part of the leaf, but nearer the apex only one bundle can be distinguished, as in Fig. 101. The wood consists of tracheids, with plates of parenchyma, resembling medullary rays, between them. The first-formed tracheids, on the upper side of the xylem, are spiral, the rest pitted; the phloëm has much the same structure as in the young stem. Between wood and bast is a layer of cambium. As compared with the leaves of most Dicotyledons or Monocotyledons, we see that the Fir leaf is very scantily supplied with vascular bundles. It has, however, an arrangement of its own, which to some extent makes good the deficiency. Among the cells of the conjunctive parenchyma there are a number of short tracheids with bordered pits (see Fig. 103, *t*). These tracheids are in communication both with one another and with the xylem of the bundle. They no doubt take up water from the bundle, and pass it on through the pitted endodermis to the assimilating tissue, where it is wanted. These tracheids outside the bundle form what is called the *transfusion tissue*, a very characteristic feature in the anatomy of coniferous leaves.

The phloëm as well as the xylem enjoys the advantage of an extension into the conjunctive tissue. On each side of the bundle we find a large group of cells with dense protoplasmic contents (see Fig. 103, *al*). They join on to the phloëm of the bundle. These *albuminous* cells, as they are called, appear to answer the same purpose as the enlarged companion-

cells at the ends of the finer bundles in dicotyledonous leaves. It is supposed that they collect the protein substances formed in the mesophyll, and transfer them to the phloëm for transport into the stem.

The conjunctive tissue further contains a strand of thick-walled fibres placed just outside the phloëm (see Fig. 101). We see, then, that the tissue of the cylinder is altogether rather complicated, for besides the vascular bundle and the ordinary parenchymatous cells, in which starch is formed, it contains the transfusion-tracheides, the albuminous cells, and the sclerenchymatous fibres.

The leaves remain on the tree for three or four years. During this time a certain amount of new tissue, chiefly phloëm, is formed by the cambium. Secondary growth in a leaf is not so very common, and is limited to leaves which last for a long time.

The leaf is constricted at the base, so that the mesophyll here comes to an end. Only the cylinder extends through into the stem. Hence all the food-material which goes to and fro between leaf and stem must pass through the tissues of the cylinder, which thus forms part of the conducting system of the plant.

The scale-leaves which protect the buds have a very simple structure compared with the foliage-leaves, for they have no assimilating work to do. They often contain no vascular bundle at all; two resin canals, however, are present in the mesophyll. The epidermis on the outer surface of the scale has an extremely thick cuticularised external wall, and this is no doubt the most important part of the whole

scale-leaf, as it protects the young organs of the bud from the risk of drying up.

c. Root

The root-system of the Spruce, and of Conifers in general, consists of the main tap-root and its

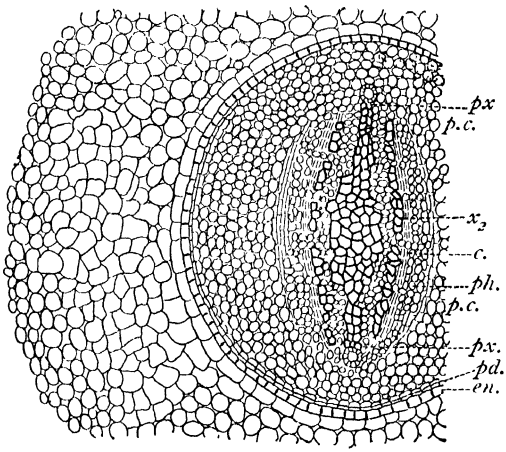


FIG. 104.—Transverse section of the root of *Picea excelsa* at the commencement of secondary thickening. *px*, *px*, the two protoxylem groups; uniting them is the primary xylem-plate. Outside each protoxylem group is a resin canal. x_2, first layers of secondary xylem; *c*, cambium; *ph*, phloem; *p.c*, pericycle; *pd*, periderm; *en*, endodermis. Outside this is cortex. Magnified 33. (R. S.)

branches. Adventitious roots hardly ever occur in these plants, unless it be on the base of the hypocotyl, where they scarcely differ from the ordinary rootlets.

The general structure of the root is of the dicotyledonous type—that is to say, we find as a rule a

simple primary structure with a small number of strands of wood and bast. This simple primary structure soon becomes completely transformed by the early occurrence of secondary growth on a great scale. The mode of development is like that of a Dicotyledon, and consequently the resulting structure

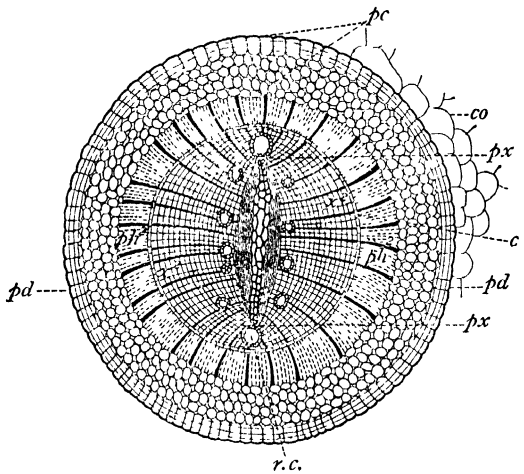


FIG. 105.—Semi-diagrammatic transverse section of a root of *Picea excelsa* at a later stage. *px*, *px*, protoxylem groups; *r.c*, resin canal; x^2, secondary wood; ph^2, phloem; *pc*, pericycle; *pd*, periderm, formed from outer layer of pericycle; *co*, remains of cortex. Magnified 22. (R.S.)

is also similar. We have found many such resemblances in the vegetative organs, though as we shall see, the two Classes are not at all closely related. The young root is clothed on the exterior by a piliferous layer of thin-walled cells. The root-hairs, however, remain short (Fig. 108, *r.h*). The Coniferæ

generally are badly provided with root-hairs, and many species do not form them at all. Root-hairs increase the absorbent surface by which water can be taken up. The greater the transpiration, the greater is the quantity of water needed, and the more does the absorbent surface require to be increased. Now the leaves of most Coniferæ have a very thick cuticle, while the stomata are not very numerous and lie sheltered at the bottom of deep depressions. The water-conducting tissue of the leaf is also, as we have seen, but moderately developed. Hence the amount of water vapour given off in transpiration is comparatively small, and the supply of water taken up is small in proportion. Instead of root-hairs being present many coniferous roots are closely surrounded by fungal hyphæ, which absorb water and substances in solution from the soil and pass these on to the roots. Such an association between a fungus and the root-system of a plant is termed *mycorrhiza*.

Within the piliferous layer is a wide zone of parenchymatous cortex, limited on the inner side by the endodermis, which immediately surrounds the central cylinder (see Fig. 104). This endodermis has the structure with which we have already become familiar. Its radial and horizontal walls are corky and undulated, and show the characteristic dark line when seen in section (see Fig. 109, *en*).

The cylinder of the root in the Fir may be either triarch or diarch. The main-root always has the former structure. We will describe the diarch type which our figures illustrate. The triarch roots do not differ from this except in the number of bundles.

The first thing that strikes us as peculiar in the structure of the cylinder is the great width of the pericycle, which forms a broad zone from six to nine cells in thickness. It is thickest opposite the middle of the two phloëm groups (see Fig. 104, *p.c*). Most of the pericyclic cells contain a quantity of starch, which is ready for use in the formation of the cell-walls of the new tissues as they develop. Within the pericycle comes the vascular tissue, which, as seen in transverse section, occupies a somewhat elliptical area (see Fig. 104). The two protoxylem groups lie at the ends of the long axis of the ellipse, and therefore at the points where the pericycle is narrowest (Fig. 104, *px*). This first-formed xylem consists of spiral tracheids. The tissue lying between the two protoxylem groups slowly becomes converted into wood. The differentiation advances from either end towards the middle of the cylinder, until ultimately a continuous plate of primary wood is formed, extending across the middle of the cylinder (see Figs. 104 and 105). The primary wood is now complete. Its development goes on very gradually, so that the secondary growth has usually begun before the primary structure is finished. We will, however, consider the two stages separately. All the middle part of the primary plate of wood consists of pitted tracheides. Just outside each protoxylem group a resin canal is formed in the pericycle (see Figs. 104, 105, and 106).

The primary phloëm forms two bands, one on each side of the xylem-plate, from which they are separated

by a few layers of conjunctive parenchyma (see Fig. 104, *ph*).

Even before the primary tissues are completely developed, cambium begins to arise by tangential

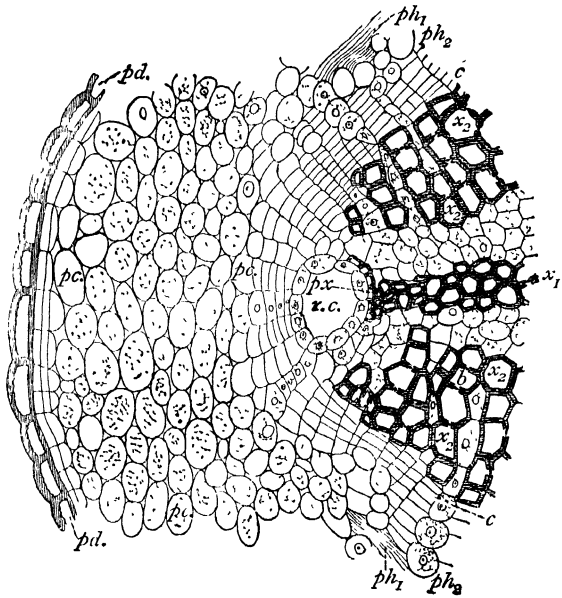


FIG. 106.—Part of a transverse section of the root of *Picea excelsa*, showing the completion of the cambium outside the protoxylem by division of pericyclic cells. *px*, protoxylem; x_1, primary xylem-plate; x_2, secondary xylem; *b*, bordered pits; *c*, cambium; ph_1, primary phloëm (crushed); ph_2, secondary phloëm; *r.c*, resin canal; *pc*, pericycle; *pd*, periderm. Magnified 165. (R. S.)

divisions of the conjunctive cells lying just inside the phloëm groups. As usual, secondary wood is formed on the inner side of the cambium and

secondary bast on its exterior. As it is the layer of cells next the phloëm which divides to form the cambium, a band of unaltered parenchyma is always left between the primary and secondary wood (see Figs. 104, 105, and especially 106).

For some time the cambial divisions are limited to the part immediately within the phloëm groups (see Fig. 104). Eventually, however, the division spreads to the pericyclic cells lying outside the two resin canals, which border on the protoxylem groups. In this way the cambium is completed round the ends of the xylem-plate, and henceforward it forms a continuous ring. Fig. 106 represents the stage when the cambial divisions have already extended to the cells beyond the resin canal. No secondary tissue has as yet been formed in this position, although at the sides of the xylem-plate a considerable amount of secondary wood and bast has already been developed, so that the primary phloëm is crushed and obliterated. A later stage, in which the secondary tissues already form a complete ring, is shown in the diagrammatic figure 105. The structure of the secondary tissues needs no special description; it is the same as in the stem. We may, however, notice that in the first few layers of the secondary wood the pits are formed on all surfaces of the tracheids indiscriminately (see Fig. 106, *b*). In the later-formed layers they are limited to the radial walls (see, however, p. 245).

As soon as the cambium has begun its activity, the most external layer of the pericycle also becomes the seat of new formations. The cells of this layer divide

up by tangential walls, and thus give rise to a phellogen which forms cork-cells on its outer side (see Figs. 104, 105, 106, *pd*). From this time onwards the root ceases to be an absorptive organ. The corky periderm completely isolates the cortex from all communication with the conducting cylinder, and consequently the whole external tissue, from the endodermis outwards, dies away. Henceforward the root is an organ of conduction only, consisting solely of the central cylinder, which by means of its cambium retains the power of unlimited growth. In all these respects the root of a Conifer agrees closely with that of a typical Dicotyledon.

d. Growing Points and Lateral Appendages

a. Growing-Point of the Stem

The apex of the shoot in a Fir has essentially the same structure as that of an angiospermous plant. It consists of meristem, the cells of which are small, and have the usual characteristics of embryonic tissue, large nuclei, abundant cytoplasm, and thin cell-walls (see Fig. 107).

The formative layers of the meristem are less distinct here than in Angiosperms. Whereas in the latter it is a general rule that the external layer of the apical meristem gives rise to the epidermis only, this is not the case in Conifers. Here the superficial cells of the growing-point may divide by walls parallel to the surface, and thus contribute to the formation of cortical as well as of epidermal tissue

(see Fig. 107). The limit between plerome and periblem is often impossible to trace near the apex. Thus in our figure the sharp line of demarcation at *p* corresponds to the limits of the pith, not to those of the plerome. Without entering further into the question of the meristematic layers, which is a difficult and disputed one, we may safely say that their differ-

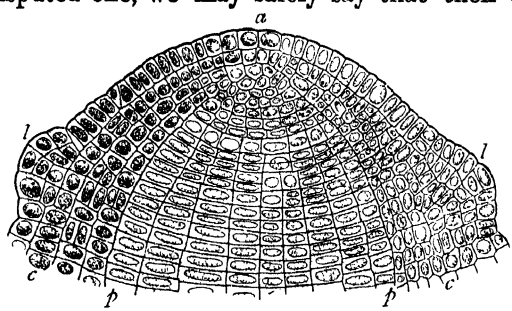


FIG. 107.—Median longitudinal section of the growing point of the stem of *Picea excelsa*. *a*, apex; *l*, *l*, very young leaves; *p*, *p*, young pith; *c*, *c*, cortex. Between *c* and *p* the vascular bundles arise. Magnified about 140. (After Sachs.)

entiation at the apex of the stem is on the whole less sharp in Gymnosperms than in Angiosperms.

The leaves and branches arise, just as in Angiosperms, exogenously, *i.e.* they are formed by the growth and division of cells which belong to the outer layers of the meristem (see Fig. 107, *l*, *l*). Their tissues are always in direct continuity with those of the shoot which bears them.

β. Growing-Point of the Root

The apex of the root in the Spruce and its allies grows in much the same way as that of a Dicotyledon

There is an outer layer of meristem (the *calyptrogen*) forming both the root-cap and the piliferous layer (see Fig. 109, *c*), a middle group or *periblem*, which gives rise to the cortex (*p* in Fig. 109), and within this is the *plerome*, from which the central cylinder is developed (*pl* in same figure). This, at least, is the arrangement at the apex of young roots, such as those shown in Figs. 108 and 109, soon after their first formation. It is doubtful whether the limit between the periblem and the calyptrogen can always be traced at the growing point of the older roots.

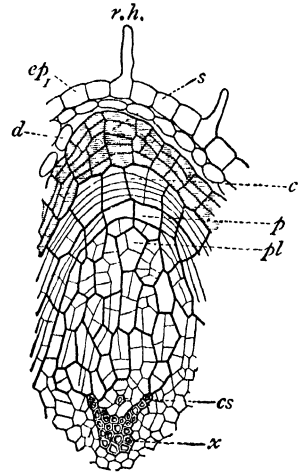


FIG. 108.—Portion of a transverse section of a root of *Pinus Pinea* (allied to *Picea*), showing an early stage of development of a rootlet. *x*, protoxylem group of main root; *c.s*, resin canal; *d*, remains of cortex of main root; *ep*, its piliferous layer, in which root-hairs, *r.h*, are shown; *pl*, plerome of rootlet; *p*, periblem; *c*, calyptrogen; *s* (shaded), digestive sac, covering the apex of rootlet, and formed from the outer layer of the pericycle of the main root. Magnified about 150. (After Van Tieghem and Douliot.)

The formation of the rootlets or branches on the parent-root also follows the dicotyledonous type, with slight modifications. The rootlets are arranged in as many vertical rows as there are protoxylem groups in the main root. Thus, in our diarch root of the Spruce there would be two opposite rows of rootlets lying in the same

plane as the xylem-plate. The rootlet here, as in all Flowering plants, arises from the pericycle of the main root. The layer of pericyclic cells which divides to form the rootlet is here the second layer from the outside. Tangential walls are first formed, which separate off the plerome, or future central cylinder of the rootlet, while the outer cells resulting from the first division again divide tangentially into

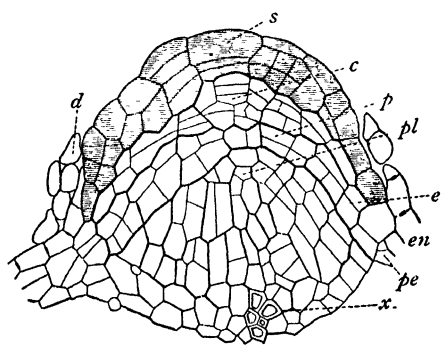


FIG. 109.—Similar section of a root of *Picea excelsa*, showing origin of a rootlet. *en*, endodermis of main root; *pe*, outer layers of pericycle; *e*, cortex at base of rootlet; other lettering as in Fig. 108. Magnified about 150. (After Van Tieghem and Douliot.)

periblem and calyptrogen. The more internal layers of the pericycle merely form the base of the central cylinder of the rootlet, by which it is attached to the vascular tissue of the main root.

The outermost layer of the pericycle also divides, and follows the growth of the young branch, round which it forms a temporary envelope (*s* in Figs. 108 and 109) during its growth through the cortex. This envelope is the *digestive sac* (see p. 171).

The whole of the cortex, as well as the piliferous layer, has to be bored through by the rootlet before it reaches the exterior. It completely absorbs all the tissues which lie in its way.

The only peculiarities in the mode of origin of the branches of the root, in this instance, depend on the fact that the pericycle is of unusual thickness, and are not characteristic of the class generally, but only of the Spruce and its nearer allies. In all the essential points the mode of branching of the root is identical in Gymnosperms and in Dicotyledons.

Summary of the Vegetative Structure of Conifers

In the general morphology and anatomy of both stem and root the Conifers agree closely with Dicotyledons, while they bear little or no resemblance to the Monocotyledons. The distribution and longitudinal course of the vascular bundles and the mode of secondary growth are practically identical in Conifers and Dicotyledons. Yet in other respects we find very great differences. This is especially the case as regards the leaves.

Some Conifers have leaves of more complex structure than those of the Fir, but still it is characteristic of the group to have a comparatively simple bundle-system in the leaf. Its simplicity is constantly compensated for by the formation of transfusion tissue and albuminous cells outside the actual bundles.

In the more minute structure there are also important differences; the entire absence of vessels from the wood is a striking character

As regards the phloëm, we find distinctive peculiarities in the structure of the sieve-tubes, and in the replacement of true companion-cells by elements of a different origin. These characters suggest to us that after all we are dealing with a group fundamentally distinct from Dicotyledons. It will be noticed that in the points in which Conifers differ most strikingly from Dicotyledons, they differ equally from Monocotyledons. We shall find later on that in some peculiarities of their vegetative structure the Conifers approach certain families of the Flowerless Plants, which we have yet to consider.[1]

The study of the vegetative organs of these plants, however, throws comparatively little light on their real systematic position. We will now proceed at once to make ourselves acquainted with their reproductive phenomena.

III. *STRUCTURE OF THE REPRODUCTIVE ORGANS*

a. The Male Cone

The male cone of the Fir, as we have already learnt, is a short lateral shoot, bearing a few bracteoles on the lower, and numerous spirally-arranged stamens on the upper part of its axis.

In form, the stamens are more obviously leaf-like than those of Angiosperms. The pollen-sacs are only two in number on each stamen, and are inserted side by side on its under surface. In some other Conifers, however, they are much more numerous. While in Angiosperms the number of

[1] See Part II. (Flowerless Plants).

the pollen-sacs on the stamen is very constantly four, in the Gymnosperms their number is subject to very great variations. The dehiscence of each ripe pollen-sac takes place separately by a longitudinal slit.

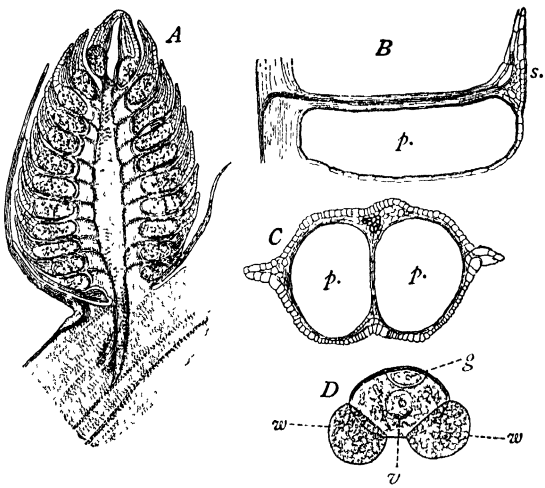


FIG. 110.—*A*, Male cone of *Pinus pumilio* in median longitudinal section. Magnified about 7 times. *B*, Longitudinal section through a single stamen, showing one of the pollen-sacs (*p*) below: *s*, apex of lamina. Magnified 14. *C*, Transverse section of a stamen: *p*, *p*, the two pollen-sacs. Magnified about 20 times. *D*, A ripe pollen-grain: *g*, small generative cell; *v*, large vegetative cell; *w*, wings formed by inflated cuticle. Magnified 290 times. (After Strasburger.) For details of pollen-grain, see Fig. 111.

Each pollen-sac arises from a small group of cells on the under side of the stamen while it is still very young. One cell of this group, lying immediately below the epidermis, becomes the *archesporium*, and

after dividing up a great many times, gives rise to a large mass of pollen mother-cells. Here, as in Angiosperms, the pollen-producing tissue grows at the expense of the surrounding layers; the innermost of these layers, called the tapetum, is rich in proteins, and is the first to be digested. The outer wall of the pollen-sac is originally about three cells in thickness, but before maturity all except the epidermis have disappeared (see Fig. 110, B, C).

The division of the pollen mother-cells takes place in the early spring. Each mother-cell divides into four daughter-cells, which become the pollen-grains. An enormous number of pollen-grains are produced altogether. If we shake a Fir-tree in May, when the male flowers are ripe, the pollen comes out in great clouds of yellow dust, which float for a long time in the air, and are carried to great distances if any wind is blowing. The Firs are *wind-pollinated* trees —that is, the transport of the pollen-grains from the stamens to the ovules is entirely dependent on currents of air. Hence a very small proportion of the pollen-grains ever reach the ovules, and in order that there may be a fair chance of pollination taking place at all, a very large number must be produced, the vast majority of which are wasted. We will now see why the pollen-grains are so light and float so long in the air. If we examine the ripe pollen-grains under the microscope, we find that each grain has a curious winged form, owing to the development of two large air-cavities in the cell-wall (see Fig. 110, D, *w*). The wall of the pollen-grain is covered on

the outside by a layer of cuticle. At two places on opposite sides of the grain the cuticle becomes separated from the cellulose wall within; the spaces thus formed are at first filled with water, so that a kind of blister arises on each side of the pollen-grain. The water is absorbed and the spaces become filled with air when the pollen is ripe. This curious arrangement has the effect of reducing the weight of the pollen-grain in proportion to its surface, these lateral expansions acting as veritable wings. Thus the grain is more easily carried to a distance by the wind.

Before the pollen-grain is ripe, important changes go on in its interior. Each pollen-grain, when first formed by division of its mother-cell, is merely a single cell with one nucleus. But before the dehiscence of the pollen-sac takes place, a series of divisions goes on in each pollen-grain. First, a small cell is cut off on the side of the grain farthest from the insertion of the wings. This little cell is separated from the large one by a thin wall shaped like a watch-glass. Two more divisions take place in the large cell, cutting off two more small cells, so that there is now a row of three small cells placed one upon another, and projecting into the cavity of the large cell. The first two of the small cells collapse, the third grows bigger and divides into two, forming a little stalk-cell and a larger terminal cell, which is long enough to reach quite half way across the cavity of the grain (Fig. 111, *A* and *B*).

The pollen-grain is now ripe, and we see that

within its winged membrane no less than five cells are enclosed: first, the large cell, which still forms the main part of the whole; second and third, the two little collapsed cells next the wall; fourth, the stalk-

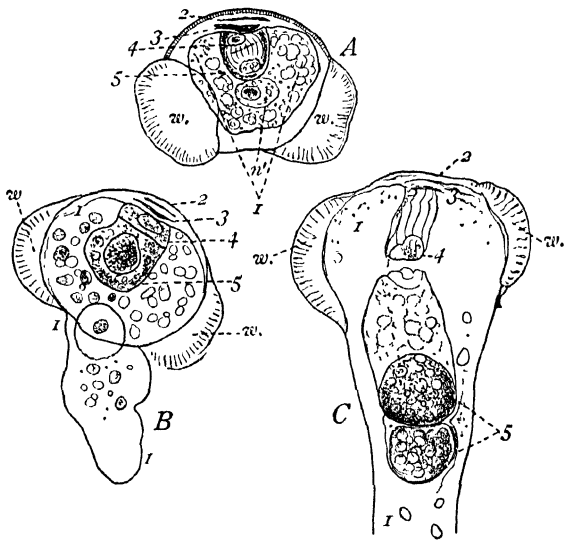


FIG. 111.—*A*, Pollen grain of *Picea excelsa* shortly before it is ripe. *w*, *w*, the wings; 1, the large vegetative cell; its protoplasm is contracted; n^1, its nucleus; 2, 3, the two collapsed cells; 4 and 5, the stalk-cell and terminal or generative cell, not yet completely divided from one another. *B*, Pollen-grain beginning to germinate. The large cell, 1, is growing out to form the pollen-tube. Lettering as before. *C*, Germination more advanced; only upper part of pollen-tube shown. The generative cell, 5, has divided into two, each with a very large nucleus. Magnified 240. (After Strasburger.)

cell; fifth, the terminal cell. We see, then, that the pollen-grain of a Fir is a much more complicated structure than that of an Angiosperm (see Fig. 111).

b. The Female Cone

The arrangement of the organs of the female cone has already been described.

We have seen that each of the conspicuous scales of the cone is an outgrowth produced on the upper surface of a much smaller scale, which may be considered to represent a carpel. Hence we may call the little scales first formed, the *carpellary scales.* The much larger outgrowths which they bear, and which in their turn bear the ovules, are called the *ovuliferous* or *seminiferous scales.* The latter may be regarded as forming a placenta, which in this case much exceeds in size the carpel which produces it.

There is, however, much uncertainty as to the interpretation of the parts of the female cone in Coniferæ.

In the Firs two ovules are borne on the upper surface of each ovuliferous scale. Neither the number nor the position of the ovules is at all constant in the Coniferæ generally. In the Araucarias, for example, to which the "Puzzle Monkey" belongs, there is only a single ovule to each carpellary scale, while in some of the Cypress family a great number are produced on each. The ovuliferous scale is often rudimentary or absent, as in the Araucaria family, where the ovule is born directly on the carpellary scale. In the Yew, which is classed with Conifers, though it does not bear cones, the ovule is not formed on a leaf at all, but is seated on the end of a short branch.

To return to the Fir: each ovule is straight (*orthotropous*), and has a single integument. The micropyle points inwards towards the axis of the cone.

It is not necessary to follow the early development of the ovule in detail, for up to a certain point it grows in very much the same way as the ovule of an Angiosperm. If the reader will refer to the development of the ovule (see pp. 118 and 180), as described in the Wallflower or the Lily, he will understand what goes on here. Here, as in Angiosperms, the important changes all go on in the nucellus or middle part of the ovule. The archesporium arises from a cell just below the epidermis of the nucellus. The archesporium is a single cell to begin with. It divides by a tangential wall; from the upper part *tapetal* cells are formed. The lower part divides up into a row of three cells, and it is usually the lowest of the three which becomes the embryo-sac. Both the epidermis and the tapetal cells undergo a great many divisions by tangential walls, so that the embryo-sac comes to be buried deep down in the nucellus, beneath a thick mass of tissue.

The embryo-sac at first, like any other cell, has a single nucleus, which soon divides up repeatedly, until there are a large number of nuclei in the protoplasm lining the cell-wall of the sac. These nuclei are at first free, but after a time cell-walls are formed between them, cutting up the parietal layer of protoplasm into a layer of cellular tissue. The cells thus formed continue to grow and divide until the whole embryo-sac is filled with tissue. The growth of the sac still goes on, until by the time of fertilisation, in the latter part of June, it is about $\frac{1}{8}$ of an inch in length. The growth and cell-division of the internal tissue keep pace with the enlargement of the embryo-sac.

We see, then, that in the Fir, *the embryo-sac becomes filled with tissue before fertilisation.* This characteristic is common not only to all Conifers, but to all Gymnosperms, and is one of the most important distinctions between this Class and all other Flowering Plants. The tissue within the embryo-sac has the same function as the endosperm of the Angiosperms, and is often called by the same name, but, as its origin is so different, it is better to use a distinct term, and call it the *prothallus* (see Part II., *Flowerless Plants*).

After the embryo-sac is filled with tissue, but before it has reached its full size, certain cells of the prothallus, at the end towards the micropyle, begin to be distinguished from their neighbours by their larger size and denser protoplasm. These cells are from three to five in number, and are always superficial cells of the prothallus, in contact with the embryo-sac wall at its upper end.[1]

While the neighbouring cells go on dividing as fast as they grow, these few special cells grow enormously without dividing. After a time, however, each of them divides near its upper end by a transverse wall. The upper and smaller daughter-cell thus formed undergoes several further divisions, both transverse and longitudinal. The lower cell remains for a long time undivided, but continues to increase greatly in size.

The stage which we have now reached is this: the embryo-sac has grown to a great size, and is filled with tissue. At its upper end are from three to five

[1] We always use the word *upper*, in describing an ovule, for the end towards the micropyle, without reference to the position which the ovule may happen to occupy.

groups of cells, each consisting of a single very large oval cell below and a well-defined column of small cells above; each group is called an *archegonium*. The large lower cell is the *venter* of the archegonium; the little column of cells above is the *neck*.

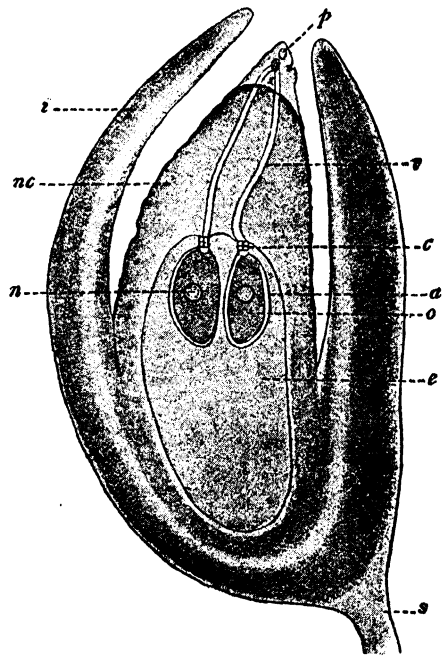


FIG. 112.—Longitudinal section of an ovule of *Picea* at the time of fertilisation. *i*, integument; *nc*, nucellus; *s*, part of the wing; *p*, pollen-grains on the tip of the nucellus; *t*, pollen tubes; *c*, neck of an archegonium; *a*, venter of archegonium containing the ovum, *o*; *n*, nucleus of ovum; *e*, prothallus. Magnified 9 times. (After Strasburger.)

A general idea of the structure of the whole ovule at this period is given by Fig. 112. In this we see

the pointed nucellus, *nc.* Most of its lower part is occupied by the large oval embryo-sac, which is shaded to indicate that it is filled with prothallus, *e.* Two of the archegonia are shown in section.

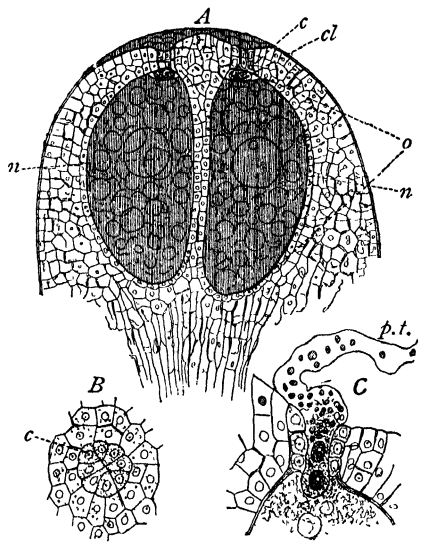


FIG. 113.—*A*, Upper part of embryo-sac in longitudinal section, showing two archegonia: *o*, ovum of an archegonium; *c*, neck; *cl*, ventral canal cell; *n*, *n*, nuclei of the two ova. *B*, Portion of upper surface of prothallus, showing the neck of an archegonium, *c*. *C*, Enlarged longitudinal section passing through the neck of an archegonium at the time of fertilisation. The pollen-tube, *p.t*, has penetrated the neck. Near the lower end of the tube its two generative nuclei are seen. Magnified—*A*, about 50 diameters; *B*, about 125 diameters; *C*, about 125 diameters. (After Strasburger.)

The archegonia are the true female organs, in which fertilisation takes place. Just before the archegonium

is ready for fertilisation, a very small lens-shaped cell is cut off from the venter at its upper end. This is called the *ventral canal cell* (see Fig. 113, *A*, *cl*). The immensely larger lower cell which remains after this final division is the *ovum* itself, which will give rise to the embryo after fertilisation. The ova in the Fir and in most Gymnosperms are of relatively very large size, so as to be easily visible to the naked eye. The large scale of the whole reproductive apparatus at the time of fertilisation is convenient for observation, but is sometimes puzzling when we have become accustomed to the minute size of the corresponding organs in Angiosperms. Fig 113, *A*, shows the upper part of the embryo-sac with two archegonia embedded in the prothallus.

Each ovum has a large nucleus, and is densely filled with protoplasm, in which there are numerous vacuoles, often bearing a deceptive resemblance to nuclei.

The neck of the archegonium, as seen in longitudinal section, consists of two to four tiers of cells (Fig. 113, *A* and *C*). When seen in surface view (Fig. 113, *B*), it appears as a rosette of six or eight cells, so that the total number of cells in the neck may vary from twelve to thirty-two.

We see, then, that the arrangements within the embryo-sac at the time of fertilisation are totally different in Gymnosperms from those in all other flowering plants. On the other hand, they agree closely with the corresponding structures in some of the higher Cryptogams. We must now consider the processes of pollination and fertilisation.

c. Pollination and Fertilisation

Pollination, as we have already learnt, is brought about by the wind, which blows the light winged pollen-grains in all directions, so that some of them chance to alight on the female cones. This takes place in May. Just before this happens, an interesting change may be observed in the cones, which prepares them to receive the pollen. The axis of the cone elongates a little throughout its whole length, so that the ovuliferous scales are all shifted a little farther apart. Thus an open space is left between each two successive scales, through which the pollen-grains can reach the ovules.

At this time the ovule is still at an early stage of development. The embryo-sac is still small, and is not yet filled with prothallus.

The integument opens widely, leaving an open passage through the micropyle, leading down to the apex of the nucellus. At the same time a small quantity of liquid is secreted within the micropyle on the surface of the nucellus. Some of the pollen-grains carried by the wind pass between the ovuliferous scales and come to rest on the edge of the integument of an ovule. Another change now takes place: the micropyle closes, the lips of the integument bending inwards, and bringing the pollen-grains into contact with the top of the nucellus, to which they adhere owing to the liquid which has been secreted.

The germination of the pollen-grain now begins. Our Fig. 111, *B*, shows a pollen-grain, highly magnified,

at the beginning of this process. The large vegetative cell sends out a tube, which penetrates the tissue of the nucellus. The vegetative nucleus passes into the tube, but becomes disorganised, and has no further part to play. So far the group of small cells within the grain has remained unchanged. Now, however, the end cell of the group, which is the generative cell, divides into two. The stalk-cell behind them breaks down; the two generative daughter-cells are set free and pass into the pollen-tube (see Fig. 111, *C*, 5). Their nuclei have now become very large and granular.

Pollination takes place in May, fertilisation not until near the end of June; the interval in the Spruce Fir is thus about six weeks. In some other Conifers, such as the Scotch Fir, *Pinus sylvestris*, and the Juniper, the interval is very much longer; the pollen falls on to the ovule in May of one year, but fertilisation is not effected until June of the next year.

To return to *Picea*: the pollen-tubes eventually grow down through the nucellus as far as the embryo-sac. They contain numerous starch-grains, which serve as food during their growth.

In the meantime the ovule has ripened. By the time that the pollen-tubes have reached the embryo-sac, it is completely filled with prothallus, and the archegonia have been formed (see Fig. 112). After the 20th of June the actual fertilisation takes place. A pollen-tube penetrates the wall of the embryo-sac just above the neck of an archegonium. It continues to grow on, passes between the cells of the neck, absorbs the ventral canal cell below, and reaches the

protoplasm of the ovum itself (see Fig. 113, *c*). The two generative cells are now at the growing end of the pollen-tube. Their nuclei are shown in the figure.

The leading generative nucleus, accompanied by a small amount of protoplasm, now passes through an opening in the membrane at the end of the pollen-tube (Fig. 114, *A*, *sn*). It traverses the intervening protoplasm and reaches the nucleus of the ovum, with which it eventually unites[1] (Fig. 114, *B*). Fertilisation is now effected. We thus see that, different as many of the preliminary processes have been, yet the act of fertilisation in itself is essentially the same as in Angiosperms. Fertilisation is, in fact, an identical process in all plants in which it occurs at all.[2]

d. Development of the Embryo

The fertilised nucleus, resulting from the fusion of the male and female nuclei, passes into the lower end of the ovum. It there undergoes two divisions, so that there are now four nuclei, all of which lie in the same horizontal plane (see Fig. 114, *C*, where, of course, only two of them are shown). Successive divisions now take place in a direction at right angles to the long axis of the ovum, until there are sixteen nuclei altogether, lying in four tiers one above another. Each nucleus of the lower three tiers is enclosed with its surrounding protoplasm within a cell-wall; the uppermost four are free nuclei (see Fig. 114, *D*, *E*). It is to be noticed that only a part of the ovum is concerned in these divisions; much the greater portion

[1] For an account of the fertilisation of certain Gymnosperms by means of spermatozoids or motile male cells, see Part II. (*Flowerless Plants*), p. 303.

[2] *Double* fertilisation, however, described above in the Lily (p. 186) is, so far as we know, a phenomenon peculiar to Angiosperms.

remains undivided, and has nothing to do directly with the development of the young plant. It only serves as a store of food for the embryo.

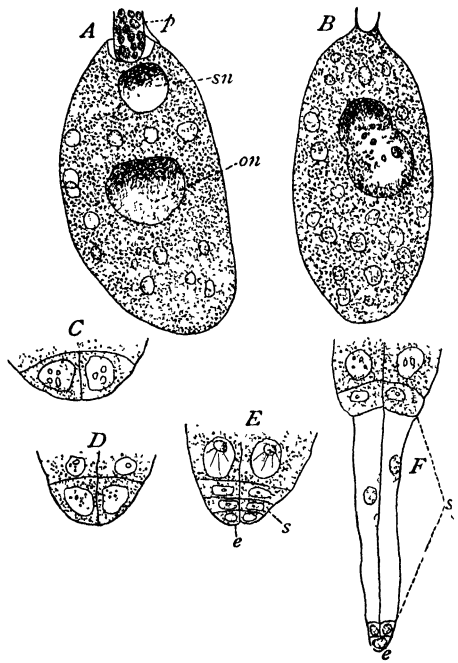


FIG. 114.—*A*, Ovum at the time of fertilisation: *p*, end of pollen-tube; *sn*, generative nucleus from the pollen-tube; *on*, nucleus of ovum. *B*, Ovum a little later: the two nuclei are in the act of fusing. *C*, Base of ovum showing first divisions after fertilisation: two of the four cells are shown. *D*, More advanced stage: four of the eight cells are shown. *E*, Still more advanced stage: *s*, cells from which suspensor will be formed; *e*, cells of the embryo. *F*, Still later stage: the suspensor *s* has grown to a great length (it is composed of four cells). The rudimentary embryo, *e*, has been pushed downward by the growth of the suspensor. Magnified about 70 diameters. (After Strasburger.)

The four free nuclei now become disorganised; the tier of four cells next below them undergoes little change, and remains in its original position. The third layer, however, *s* in Fig. 114, *E* and *F*, elongates enormously, forming the *suspensor*, which here consists of four parallel cells. The lowest group of four cells is pushed forward by the suspensor deep into the middle of the prothallus. It is this lowest group, *e* in Fig. 114, *E* and *F*, which alone forms the actual embryo.

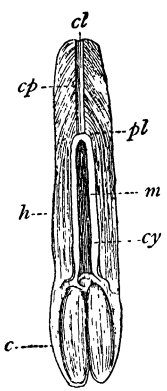


FIG. 115.—Longitudinal section of the embryo of *Picea* taken from a ripe seed. *cp*, root-cap; *cl*, central tissue of root-cap; *pl*, growing point of root; *m*, pith; *cy*, vascular tissue of cylinder; *h*, hypocotyl; *c*, cotyledons, of which only two are shown. Magnified 10 diameters. (After Strasburger.)

In the Spruce Fir only one embryo can be formed from each archegonium. All the archegonia, however, may be fertilised; so, for a time, from three to five developing embryos may be present side by side in the prothallus of the same ovule. One, however, always gains the upper hand, and in the ripe seed only this one remains. In some other Conifers, such as the Scotch Fir, the four cells of the suspensor separate from each other, and each bears a separate embryo at its end. In this case, therefore, each archegonium gives rise to four embryos, and altogether there may be from twelve to twenty in the young seed. Here also, however, only one out of the whole number comes to perfection.

We will not follow the further development of the embryo in *Picea* in detail. Its growth, with which the cell-division keeps pace, goes on from June until October, by which time the seed is ripe. The suspensor at first serves to supply the young embryo with food, but by the time the seed is ripe its function is at an end. The embryo then extends through the whole length of the embryo-sac, but is still enveloped in a mantle of prothallus; the middle part of the prothallus has been absorbed by the embryo for its own nutrition. The structure of the embryo in the ripe seed is shown in Fig. 115, which represents it in longitudinal section. The root is directed towards the micropyle. The apex of the root is protected by an enormously thick root-cap. The root itself is still but little developed, while the hypocotyl occupies nearly half the length of the embryo. The cotyledons are numerous, generally numbering about eight. This is not, however, a character common to Conifers generally, for many of them, such as the Yew, have only two. The eight cotyledons of the Firs probably represent the subdivisions of two.

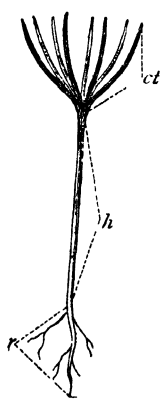


FIG. 116. — Young seedling of *Picea*. *ct*, cotyledons; *h*, hypocotyl; *r*, roots. Natural size. (After Kerner.)

The cone opens in the spring, and the winged seeds are scattered by the wind, as already described.

When the seed germinates, the root grows out

through the micropyle, and turns downward into the ground. The cotyledons during germination absorb the remainder of the prothallus. The apex of the stem directs itself upwards; the seed-coat is at first lifted up upon the cotyledons, but is soon cast off as they expand (Fig. 116). The cotyledons become green, and the young plant is now able to assimilate its own food.

Summary

We will now pass rapidly in review those facts in the reproduction and development of the Fir which are typical of gymnospermous plants generally, and which indicate their relations, on the one hand to the Angiosperms, and on the other hand to the Flowerless plants.

Apart from the peculiarities in the general morphology of the male cone, which have been sufficiently dealt with already, we find a characteristic feature in the considerable number of cells which are formed within each pollen-grain. This, as we shall see later on, is a very significant fact. The production of all these intermediate cells, before the actual generative cells are set apart, is really a cryptogamic character, and is one indication, among many, that the Gymnosperms are on a different level from all other Flowering plants.

The gymnospermy, or direct pollination of the ovule without the intervention of a stigma and style, is itself a point of great importance. Fertilisation by means of a pollen-tube is one of the chief characters of Phanerogams. In Gymnosperms we still have the pollen-tube, but its work is more limited than in

Angiosperms, for its function only consists in conveying the generative cells through the tissues of the nucellus.

On the side of the female organs, the differences as compared with Angiosperms decidedly outweigh the resemblances.

The filling of the embryo-sac with an extensive endosperm or prothallus before fertilisation is exactly what we shall find occurring in the highest Cryptogams, but is quite different from anything in Angiosperms, where only a few cell-divisions intervene between the formation of the embryo-sac and that of the ovum.

The archegonia, with their multicellular necks, are quite foreign to the typical Phanerogams, while they agree in every detail with the female organs of the higher Cryptogams. In fact, we may say that from the formation of the embryo-sac up to the act of fertilisation the whole development is cryptogamic.

The embryology, on the other hand, though highly peculiar, is not of such far-reaching significance, for the mode of development varies greatly among the Gymnosperms themselves.

The seed is still a marked phanerogamic character; after fertilisation, the differences from Angiosperms become much less striking than before.

The Gymnosperms are known, from geological evidence, to be enormously more ancient than any other Flowering Plants; they still retain many of the characters of their yet more primitive cryptogamic progenitors.[1]

[1] See Part II. (Flowerless Plants), p. 31.

GLOSSARY

ADVENTITIOUS.—Not according to rule; as in the case of roots which spring from the stem and not from the main root.

ALBUMINOUS.—1. Containing a nutritive tissue (endosperm) when ripe; used of seeds.

2. Containing protein; used of certain phloëm-cells in Gymnosperms.

ALBURNUM.—The sap-wood.

ANATROPOUS.—Bent back parallel to the funicle, so that the micropyle faces the placenta, the nucellus remaining straight; used of ovules.

ANDRŒCIUM.—The stamens of a flower, collectively.

ANTERIOR.—Turned away from the main axis.

ANTHER.—The part of a stamen which contains the pollen.

ANTHOCYANIN.—A class of pigments commonly present in the cell sap of petals and other parts of plants.

ANTIPODAL CELLS.—The cells in the basal part of the embryo-sac, away from the micropyle.

ARCHEGONIUM.—The organ in which the female cell is produced in the Gymnosperms and Higher Cryptogams.

AXIL.—The angle between stem and leaf, on the upper side of the latter.

AXILE.—Belonging to, or in the position of, the axis.

AXILLARY.—Arising in the axil.

AXIS.—The stem or main root, as distinguished from its appendages, such as leaves or rootlets.

BAST.—The tissue which conducts the food-substances formed in the leaf.

BRACT.—A small leaf in the axil of which a flower is borne.

BRACTEOLE.—A small leaf on the flower-stalk.

CALYPTROGEN.—The layer at the growing point of a root, which forms the root-cap.

CALYX.—The outermost set of leaves in the flower.

CAMBIUM.—The layer of actively dividing cells, which forms the secondary wood and bast.

CAMPYLOTROPOUS.—With the nucellus curved back so that the micropyle faces the placenta; used of ovules.

CAPSULE.—A dry, dehiscent fruit, formed of two or more united carpels.

CARPEL.—One of the innermost floral leaves, bearing or enclosing the ovules.

CARPELLARY SCALE.—The lower of each pair of scales in a female Fir-cone, bearing the ovuliferous scale on its upper surface.

CELL.—The structural unit in living organisms, consisting of cytoplasm, nucleus, and usually cell-wall.

CENTRAL CYLINDER.—The inner region of a stem or root, including wood, bast, and conjunctive tissue.

CENTRIFUGAL.—Developing from within outwards.

CENTRIPETAL.—Developing from without inwards.

CHALAZA.—The base of the nucellus of an ovule, where it joins the funicle and where the integuments are attached.

CHLOROPHYLL.—The green colouring matter of plants necessary for carbon-assimilation in sunlight.

CHLOROPHYLL-GRANULE.—A protoplasmic body (plastid) in which chlorophyll is contained.

CHLOROPLAST.—A plastid containing chlorophyll.

CHROMOPLAST.—A plastid containing a colouring matter other than chlorophyll.

COLLOIDAL.—Matter is said to be colloidal when it consists of a mixture of two phases. These may be both liquid, *e.g.* an emulsion of oil and water, or one may be solid and the other liquid, *e.g.* a suspension of clay particles in water. In each of these examples one of the phases (oil or clay) is discontinuous. A jelly (*e.g.* gelatine), however, consists of a continuous framework of gelatine with a continuous water phase permeating it (like the air spaces in a sponge). If the particles of the discontinuous phase are *extremely* small, the "system" is a true solution.

COMPANION-CELL.—A cell associated with a sieve-tube and formed from the same mother-cell.

CONJUNCTIVE TISSUE.—The tissue of the central cylinder, in which the xylem and phloëm are embedded; it includes pith, medullary rays, and pericycle.

CONNECTIVE.—The part of the anther to which the pollen-sacs are attached.

CORK-CAMBIUM.—The layer of actively dividing cells forming the cork and phelloderm.

COROLLA.—The set of leaves in a flower, next within the calyx; usually of a bright colour.

CORTEX.—The zone of tissue lying between the central cylinder and the epidermis.
COTYLEDON.—A seed-leaf; the first leaf or one of the first two leaves of the seedling.
CUTICLE.—The external layer of the outer cell-walls of the epidermis.
CYTOPLASM.—The clear, homogenous part of the protoplasm of a cell, excluding the nucleus.

DEHISCENCE.—The opening of a fruit to emit the seeds, or of an anther to emit the pollen-grains.
DERMATOGEN.—The layer at the growing-point which forms the epidermis.
DIARCH.—Having two primary groups of xylem and two of phloëm; used of roots. So also TRIARCH (3), TETRARCH (4), and POLYARCH (numerous).
DIGESTIVE SAC.—The temporary cap of a young rootlet, while still within the parent root.

ECTOPLASM.—The outer, clear layer of the cytoplasm.
EGG-APPARATUS.—The three cells (ovum and synergidæ) at the end of the embryo-sac towards the micropyle.
EMBRYO.—The young plant produced from the fertilised ovum.
EMBRYO-SAC.—The large cell of the ovule, containing, in Angiosperms, the egg-apparatus, antipodal cells, and polar nuclei, and, in Gymnosperms, the prothallus and archegonia.
ENDODERMIS.—The innermost layer of the cortex, adjoining the central cylinder.
ENDOGENOUS.—Arising from deep-seated tissues.
ENDOPLASM.—The inner, granular layer of the cytoplasm.
ENDOSPERM.—A tissue formed in the embryo-sac, to feed the embryo.
ENZYMES.—Complex substances, formed by living cells, in the presence of which certain chemical changes are rapidly effected.
EPIDERMIS.—The skin of plants; the superficial layer of tissue in stems and leaves.
EPITHELIUM.—A layer of cells secreting resin or other substances.
EXALBUMINOUS.—Containing little or no endosperm when ripe; used of seeds.
EXODERMIS.—The outermost layer of cortex in a root, just below the piliferous layer.
EXOGENOUS.—Arising from the external tissues.
EXTRORSE.—Opening outwards; used of anthers.

FASCICULAR.—Belonging to a vascular bundle.
FERTILISATION.—The union of the male cell with the female cell or ovum.
FIBROUS CELLS.—Long, thick-walled cells of the wood, serving for strength, but retaining their living contents.
FIBROUS LAYER.—The thickened layer in an anther, which brings about its dehiscence.
FILAMENT.—The stalk of a stamen.
FRUIT.—The ripened ovary, containing the seeds.
FUNICLE.—The stalk of an ovule.

GENERATIVE CELLS.—The male cells, which effect fertilisation.
GEOTROPISM.—The response of plant organs due to the stimulus of gravity.
GROWING POINT.—The part (usually the apex) of a stem or root, where the new tissues and organs are formed.
GUARD-CELLS.—The two cells of a stoma, enclosing the pore.

HAIR.—An outgrowth of the epidermis.
HERMAPHRODITE.—Containing stamens and pistil in the same flower.
HILUM.—1. The scar on a seed, where it was attached to the funicle.
2. The first-formed part of a starch-granule, round which the successive layers are deposited.
HYDROTROPISM.—The response of plant organs due to a difference in relative humidity on different sides.
HYPOCOTYL.—The part of the stem below the cotyledons.
HYPODERMA.—An outer zone of the cortex, next below the epidermis.
HYPOPHYSIS.—The cell in an embryo which joins the suspensor to the embryonic cell.

INFLORESCENCE.—A group of flowers (or a single flower) on a stem.
INTEGUMENT.—A coat or envelope of an ovule or seed.
INTERFASCICULAR.—Lying between the vascular bundles.
INTERNODE.—The portion of stem lying between two nodes.
INTRORSE.—Opening inwards; used of anthers.
IONS.—The electrically charged parts into which a molecule of an acid, base or salt, breaks up when the substance is dissolved in water.

LEAF-TRACE.—A vascular bundle, or group of bundles, passing out from the stele into a leaf.

LEUCOPLAST.—A colourless plastid, forming a starch-granule.

MEDULLA.—The pith.
MEDULLARY RAY.—A vertical plate of parenchyma running radially through wood and bast.
MERISTEM.—A tissue of actively dividing cells, from which the permanent tissues are developed.
MESOPHYLL.—The internal tissue of the lamina of a leaf, including both palisade and spongy parenchyma.
METAXYLEM.—The later-formed part of the primary wood.
MICROPYLE.—The opening in the coats of an ovule, through which the pollen-tube or pollen-grain enters.
MONŒCIOUS. — Having the stamens and pistils in different flowers on the same plant.
MOTHER-CELL.—A cell which produces other cells by division, as the mother-cell of the four pollen-grains.

NECTARY.—A gland secreting honey.
NODE.—The part of the stem to which a leaf is attached.
NUCELLUS.—The central body of the ovule, surrounded by the integuments and containing the embryo-sac.
NUCLEOLUS.—A dense mass of nuclear substance, usually present in the resting nucleus.
NUCLEUS.—A definite organ of the cell, forming part of its living substance and controlling its development and multiplication.

OCTANTS.—The 8 cells into which the embryonic cell first divides.
ORTHOTROPOUS.—Straight, not in any way bent or curved; used of ovules.
OVARY.—The part of the pistil in which the ovules are contained.
OVULE.—The young seed before fertilisation, consisting of nucellus, one or more integuments, and usually a stalk or funicle.
OVULIFEROUS SCALE.—The upper scale of each pair in a Fir-cone, borne on the upper surface of the carpellary scale and itself bearing the ovules.
OVUM.—The female cell, which, after fertilisation, gives rise to the embryo.

PALISADE PARENCHYMA.—The part of the internal tissue of the lamina of a leaf which is turned towards the light; consisting of vertically elongated cells, rich in chlorophyll.

PAPILLA.—A small outgrowth or elevation of the surface.
PARENCHYMA.—Cellular tissue, with the cells not much elongated and usually having square ends.
PEDICEL.—The stalk of a flower.
PERENNIAL.—Lasting for several years; used of herbaceous plants.
PERIANTH.—The envelopes of a flower, including calyx and corolla when both are present.
PERIBLEM.—The layer at the growing point, from which the cortex is formed.
PERICYCLE.—The outermost layer of the central cylinder, adjoining the cortex.
PERIDERM.—The secondary skin of plants, including cork on the outside and phelloderm on the inside, with cork-cambium between.
PERISPERM.—A tissue formed from the nucellus, to feed the embryo; occurring in a few seeds, *e.g.* Water-lily.
PETAL.—A leaf of the corolla.
PHELLODERM.—Secondary cortex, formed on the inner side of the cork-cambium.
PHELLOGEN.—Cork-cambium, the layer of actively dividing cells forming the periderm.
PHLOEM.—Bast; the tissue which conducts the food-substances formed in the leaf.
PHOTOSYNTHESIS.—Carbon-assimilation; the decomposition of carbon dioxide in sunlight, by the aid of chlorophyll, with the resulting formation of new organic material.
PHOTOTROPISM.—The response of plant organs due to unequal intensities of illumination on different sides.
PHYLLOTAXIS.—The arrangement of the leaves on the stem.
PILIFEROUS LAYER.—The superficial layer, bearing the root-hairs in young roots.
PISTIL.—The central organ of a flower, composed of one or more carpels, and enclosing the ovules.
PITH.—The internal tissue of the central cylinder, lying inside the zone of vascular strands.
PITS.—The thin spaces in the walls of vessels and cells.
PLACENTA.—The part of the ovary to which the ovules are attached.
PLASTID.—A protoplasmic granule, usually forming starch, and often containing chlorophyll or other colouring matter; includes chloroplasts, chromoplasts, and leucoplasts.
PLEROME.—The middle part of the tissue of the growing point, forming the central cylinder.

PLUMULE.—The young stem and leaf-bud of the embryo.
POLAR NUCLEI.—The two nuclei, one from each pole of the embryo-sac, which unite, to form, after fertilisation, the nuclei of the endosperm.
POLLEN.—The cells discharged from the stamens; they produce the male cells by which fertilisation is effected.
POLLEN-SAC.—The sac in which the pollen-grains are produced; usually there are four such sacs in the stamen of an Angiosperm and two or more in that of a Gymnosperm.
POLLEN-TUBE.—The tube which grows out from a pollen-grain and conveys the male cells to the ovule.
POLLINATION.—The depositing of the pollen on the stigma or on the ovule.
POLYPETALOUS.—With the petals separate.
POLYSEPALOUS.—With the sepals separate.
POSTERIOR.—Turned towards the main axis.
PRIMORDIAL UTRICLE.—The cytoplasm lining the cell-wall and enclosing the central vacuole.
PROCAMBIUM.—A strand of cells in the meristem of the growing point, from which a primary vascular strand will be formed.
PRO-EMBRYO.—The early stage of the embryo, when it consists of the embryonic cell and suspensor.
PROSENCHYMA.—A tissue consisting of elongated cells with pointed ends.
PROTHALLUS.—The body which bears the sexual cells; *e.g.* the "endosperm" of Gymnosperms.
PROTOPHLOEM.—The first-formed elements of the phloëm or bast.
PROTOPLASM.—The living substance of plants and animals.
PROTOXYLEM.—The first-formed elements of the xylem or wood.

RACEME.—An inflorescence consisting of a long main axis, bearing stalked lateral flowers, the lowest opening first.
RADICLE.—The young main root of the embryo.
RAPHE.—The part of the funicle which is adherent to the nucellus in an anatropous ovule.
RECEPTACLE.—The axis of a flower, on which the perianth, stamens, and pistil are borne.
REPLUM.—The persistent placenta in Cruciferiæ, to which the seeds are attached.
RESPIRATION.—The breathing of plants, involving oxidation and the giving off of carbon dioxide.
ROOT-CAP.—The sheath of protective tissue which envelops the tip of a growing root.

ROOT-HAIR.—A unicellular outgrowth of the young root, by which water and salts are absorbed from the soil.

ROOT-PRESSURE.—The osmotic pressure exerted by the cells of the root, resulting in the pumping up of water into the stem.

SEED.—The sexually produced reproductive body of the Flowering Plants, consisting of the fertilised and matured ovule, containing an embryo, with or without a nutritive tissue (endosperm).

SEPAL.—A leaf of the calyx.

SEPTUM.—1. A partition in the ovary or fruit, separating two carpels.
2. A cell-wall separating one cell from another.

SIEVE-PLATE.—The perforated cell-wall through which the cells of a sieve-tube communicate with each other.

SIEVE-TUBE.—A vessel of the bast, having perforated cell-walls between its cells.

SPERMATOZOID.—A male cell which has the power of active movement, as in most Cryptogams and in Cycads among Gymnosperms.

SPONGY PARENCHYMA.—The part of the internal tissue of the lamina of a leaf which is turned away from the light; consisting of chlorophyll-containing cells, with large intercellular spaces.

STAMEN.—The modified leaf, in a flower or male cone, which bears the pollen-sacs.

STARCH-GRANULE.—A body consisting of starch ($C_6H_{10}O_5$) and formed by a plastid.

STIGMA.—The part of the pistil which receives the pollen.

STOMA.—A breathing-pore, serving for the interchange of gases, and consisting of two guard-cells with an opening between them.

STROBILUS.—A cone, such as the male or female fructification of a Fir-tree.

STYLE.—The part of the pistil which connects the stigma with the ovary.

SUSPENSOR.—A filament of cells, forming a temporary organ of attachment for the embryo.

SYNCARPOUS.—Consisting of two or more united carpels.

SYNERGIDÆ.—The two cells accompanying the ovum in Angiosperms, and assisting in fertilisation.

TAPETUM.—The cells lining the inside of a pollen-sac, or adjoining the embryo-sac mother-cell in an ovule.

TAP-ROOT.—The main root of the plant, developed from the radicle of the embryo.

TESTA.—The seed-coat.

THALAMUS.—The receptacle.

TORUS.—The thickened portion of the closing membrane of a pit.

TRACHEA.—A water-conducting element of the wood; either a vessel (cell-fusion) or a tracheid (single cell).

TRACHEID.—A water-conducting element of the wood, formed from a single cell, not undergoing fusion.

TRANSFUSION TISSUE.—The network of short tracheids, lying outside the vascular bundle in the leaf of a Conifer.

TRANSPIRATION.—The giving off of water vapour through the stomata, from the surface of the plant, especially from that of the leaves.

TUBER.—A short and thick underground branch, serving for propagation.

VACUOLE.—A clear space in the cytoplasm, filled with cell-sap.

VALVE.—One of the segments into which the wall of a capsule splits up, on dehiscence.

VASCULAR BUNDLE.—A strand consisting of wood and bast associated together.

VENTER.—The lower part of an archegonium, containing the ovum.

VENTRAL CANAL-CELL.—The small cell lying immediately above the ovum, in Gymnosperms and the Higher Cryptogams.

VERSATILE.—Turning freely on its support, as the anther on the filament in the lily, etc.

VESSEL.—A water-conducting element of the wood, formed by the fusion of a row of cells.

WHORL.—A ring of leaves or other organs, all inserted at the same level on the axis.

XYLEM.—The wood; that part of the vascular tissue which serves principally for the conduction of water, though also for food-storage and mechanical support.

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