BOTANY FOR STUDENTS OF MEDICINE AND PHARMACY

BY THE SAME AUTHORS

ELEMENTARY STUDIES IN PLANT LIFE

AN INTRODUCTION TO THE STUDY OF PLANTS

PLANT FORM AND FUNCTION

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BOTANY

FOR STUDENTS OF MEDICINE AND PHARMACY

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PREFACE TO FIRST EDITION

THIS volume has been prepared to meet the need for an elementary treatment of Botany for the use of students of medicine and pharmacy. It is largely based on our *Introduction to the Study of Plants* and *Introduction to the Structure and Reproduction of Plants*, parts of which are reproduced in an almost unaltered form, since we feel that they present the matter in a manner equally suited to the needs of any student of the elements of the subject. In many places, however, the text has been specially modified to correspond with the requirements of the class of student for whom the book is intended, and for this reason a great deal of the matter dealt with in the works above quoted has been omitted.

We have embodied in this book the result of considerable experience in the teaching and examination of medical students, and of prolonged association with the Board of Examiners of the Pharmaceutical Society. The ordinary medical syllabus, and that of the Pharmaceutical Society's Preliminary Scientific Examination is, we believe, adequately covered. The inclusion of a chapter on Bryophyta is due to a knowledge of this group being required in certain quarters, but we do not regard it as particularly instructive to the medical student. We have endeavoured, whilst meeting particular needs, to give an adequate account of the Vegetable Kingdom from the biological standpoint, and, in pursuance of this aim, have occasionally gone somewhat beyond the scope of any existing syllabus.

We are indebted to Dame Helen H. T. I. Gwynne-Vaughan for permission to reproduce Figs. 35–37, and to Prof. Bateson, F.R.S., and Miss Pellehew, for Fig. 157. A large proportion of the figures are original. Our acknowledgments are also due to Mr. E. Hatschek for revising the matter on pp. 69–72.

F. E. F.
E. J. S.

LONDON,
February 1921.

PREFACE TO SECOND EDITION

THE present edition has been revised throughout and brought up to date. In particular the sections devoted to the physiology of plants have been considerably modified and in part rewritten. But there is no change in the scope or the manner of treatment. We are indebted to Dr. F. M. Haines for giving us the benefit of his experience on various matters relating to plant-physiology.

F. E. F.
E. J. S.

LONDON,
June 1928.

INTRODUCTION

By A. E. Boycott, M.A., D.M., F.R.S.,

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Dean Gaisford once affirmed that there were three reasons why people should know Greek. " In the first place," he said, " it enables you to read the words of our Saviour in the original, in the second place it allows you to have a hearty contempt of those who are not acquainted with the language, and in the third place it leads to positions of emolument in the church." Of his first reason it may justly be remarked that it is based on the strange assumption that Jesus talked in hellenistic Greek, of his second that it is hardly charitable, while of his third perhaps the less said the better. But for all that a little reflection suggests that the professor-dean, in the pompous and rather priggish fashion proper in his day to his position, was dimly groping at the real defence of a study through which we have reached some of our highest spiritual and practical achievements since Erasmus. He saw that Greek enabled a man to make a better living out of the world and to have the broader hold on freedom which that allows; that it admitted him to an intellectual companionship which was an aristocracy by its possession of inward resources and inspirations that others had not got; that it helped men to understand the Bible in the fullest way. I think this is what he meant; he said it in blunter words.

Anyone can for himself parody any of the current versions of Gaisford's remarks into a crude apologetic of the pursuit of any branch of knowledge which has technical applications to life as we live it—of, for example, the chemistry and physics and biology which occupy the earlier years of the medical curriculum. But the modern version—his quip is now nearly a hundred years old—is perhaps worth rather longer statement.

Taking the third and least important reason first, it is apparent that many of the sheer facts which are the data of the preliminary sciences are of direct and immediate use in practical medicine. The identification of sugar in the urine, the measurement of the pressure of blood in the arteries, the recognition of bacteria and moulds in infectious diseases are procedures of chemistry, physics and botany which are in daily use in practical medicine. An ability to understand these and a host of similar operations may not perhaps guarantee a position of emolument in the profession, but at any rate such a position is impossible without it. Then why not restrict the topics in these sciences with which the medical student is expected to familiarise himself to those which in this way have direct technical applications? Botany, for example, was at one time "useful," for it was an obviously necessary part of the training of the doctor that he should learn to recognise foxglove and deadly nightshade and monkshood when he had to collect his drugs himself. He now buys them from the druggist as digitalis, atropine and aconitine. Even now, however, a general knowledge of botany may be as directly useful to a doctor as a stethoscope. If he can distinguish the American poison vine from the common Ampelopsis he will from time to time be able to identify the cause and to achieve the cure of most distressing inflammations of the skin: if he can recognise a cruciferous plant he will know what to administer to a case of scurvy—a disease, due to errors of diet, which is cured particularly easily by plants belonging to that natural order. From the most purely utilitarian point of view, therefore, there are some things in botany that are worth knowing. And the reason why it is impossible to learn these and these only is simply that no one knows what is useful and what is not. Discovery is a process and not an event, and few things have been more striking in the progress of medicine in recent years than the way in which natural knowledge has come to be woven into its everyday work. The control of malaria and yellow fever depends on our appreciation of how certain mosquitoes live and breed, the control of plague on the habits of fleas and rats, the adequate feeding of children on the nature of the food of cows and pigs. Modern civilisation, which we all believe to be modern progress, depends so much on the successful exploitation of the natural resources of the world that no one can tell what particular item of knowledge is going to be useful—indeed, necessary—at any point in his pilgrimage. Any attempt therefore to learn what is at any one time of proved utility and to neglect everything else is bound to fail in its object: ten or twenty years of medical progress will make such changes in the list that the student who thinks himself well-equipped with practical knowledge will find as a middle-aged doctor that he knows much that is useless and is ignorant of more that is useful. Utilitarianism is sure to be its own undoing.

There are fortunately broader grounds on which the earlier years of the curriculum can rest. It is obviously a good thing for a medical man to have some knowledge of what the world is made of and how it works, because this information is an integral part of any satisfactory education. Everyone is the better for understanding the mechanism of the barometer whose indications he follows, for an acquaintance in a general way with the anatomy of the body and its way of working, for knowing something of the rare metals which go to make the nib of his fountain pen, for some idea of how a cabbage grows. A man who holds that the ups and downs of his weather-glass are vagaries of the devil, or that the œsophagus leads into the lungs, or that chalk is made of iron, can never be a fit member of a profession which requires more than most an imaginative and sympathetic understanding of the world and the people in it—requires, in short, an educated mind. One of the special qualifications which a training in the preliminary sciences is apt to give is what is known as a "scientific" habit of mind. By this we simply mean the habit of drawing reasonable conclusions from premises of which one is reasonably sure, of adding two and two together so that they make four instead of five, of instinctively looking for the causes of effects and the effects of causes. It is by no means the prerogative of the natural sciences. The scientific method may be applied to irregular Greek verbs or to Roman history or any other matter of human interest just as much as to chemistry or physics or biology. Its more immediate association with the natural sciences is due to the fact that scientific subjects are generally susceptible to experimental inquiry while the humanities are not, and that it is by the experimental method that we have convinced ourselves that the "scientific" habit of mind gives us the best approximation we can make to the truth. An educated man must have the scientific habit of mind, and a doctor must be an educated man. He will not have a hearty contempt for his less fortunate brothers, but he will understand them better.

But a doctor ought to have a more ample acquaintance with these sciences than the educated man in the street. Medicine is a piece of applied biology and requires a generous training in the broad principles which summarise the relations of live things to one another and to inorganic nature. The interactions of animals with plants, and plants with one another, of all life to the dead background on which the real world moves, are immensely complex: to understand the life of a dandelion or an earthworm is difficult enough, but serious attention to what is known of these relatively simple cases is a necessary introduction to any attempt to understand how man lives and moves and has his being in a world which he has made more and more complicated for himself by progressively trying to wriggle out of the rules of nature. Any medicine which does not live in a biological atmosphere must be a maimed business, and the medical student cannot saturate himself too fully with the notions of biology. The mouth contains an assemblage of minute animals and plants which live in community with one another and with the man who furnishes a warm wet habitat for them; the large intestine provides different conditions and has quite another series of species; the dry exposed skin on the surface of the body has another. The harmonious relations of these bacteria and protozoa with one another and with their host are liable to go awry and any of the parties concerned may come to some damage. This is a special case of the general problem which botanists call œcology, and why different societies of bacteria live in the mouth, the rectum and the skin is just the same question as why different associations of higher plants give their characteristic appearances to oak woods, moors and marshes. To understand either question one must consider both. In some instances biology will explain medicine, in other cases medicine will illuminate biology. One of the most moving axioms of biology is that the world is an harmonious whole: no live thing—and no part of a live thing—lives for and by itself, and if the routine of its being is varied it will still achieve, or at least attempt, the maintenance of this harmony. Correlation, adaptation and compensation are seen easily enough when we look at the world, but the experiments which convince us that this interpretation of nature is the right one are to be found especially in the field of medicine. In the presence of any disease or injury a live thing will do its part to put itself right again: a cut finger heals if it is left alone, a pencil does not sharpen itself. The business of practical medicine is to make people feel better, and it does this by helping on the natural processes of repair and restoration which are common to man and the earthworm: the mending of a broken leg depends on what the body does, the mending of a broken bicycle on what the engineer does. If anyone wants to play a good doctor's part in the running of this wonderful pageant, he ought to know biology, he wants to read his patients in the original. Besides, it makes medicine so much more amusing.

CONTENTS

CHAPTER I

THE PLANT CONSIDERED AS A WHOLE

OF the two great groups of living organisms, plants are specially suited to cultivating the power and habit of observation. Their study, moreover, serves to broaden the outlook on living things in general, for animals and plants have many features in common which are inseparable accompaniments of life. Such are the phenomena of growth and breathing, and the fact that new individuals, in both groups, originate from pre-existing individuals. In all cases, too, there is but a limited span of life, ultimately followed by death and consequent decay.

The Vegetable Kingdom includes a great variety of forms, of which some are exceedingly small and simple in structure, whilst others, as, for instance, the flowering plants, may attain a large size and are relatively complex.

A good example of such a flowering plant is afforded by the Shepherd's-purse (*Capsella bursa-pastoris*), which is exceptionally common on waste ground at all times of the year (Fig. 1). It soon appears on exposed soil that is not carefully tended, increasing very rapidly and successfully competing with other plants growing in the same situation. In short, it possesses some of the distinguishing characteristics of a weed, and will serve to make us familiar with the broad features of a plant.

Observation teaches us that this, like all flowering plants, has two distinct parts which clearly live under very different conditions. One part, the *shoot*, consisting of the stem bearing leaves (Fig. 1, *Sh.*), is situated overground, being surrounded on all sides by the air and exposed during the daytime to the light of the sun. The other part, the *root* (Fig. 1, *Rt.*), is situated underground, is completely embedded in the soil, and consequently lives in darkness. It is not difficult to find further points of distinction between shoot and root. Thus the parts of the shoot (stem and leaves) are green, whereas the root and its branches are white. The branches of the root are all similar in appearance, but the stem bears different kinds of branches, some of which are round and slender like itself, while others are broad thin flat structures known to us as leaves. Other differences will become apparent when we have studied these two parts of the plant in greater detail.

On examining the root more closely we find that there is a main portion (Fig. 2, *m.a.*) which is a direct downward continuation of the stem, its position being therefore more or less vertical. This, the main axis of the root, bears side-branches (the *lateral roots*, Fig. 2, *l.r.*^{1}) which grow outwards and slightly downwards, so that they stand at an acute angle. In older plants the lateral roots bear further branches (Fig. 2, *l.r.*^{2}, *l.r.*^{3}) which spread out in all directions.

A short distance behind the tips of the main root and its branches careful examination with a lens may show a number of very short colourless hairs (the *root-hairs*) which, however, can be much more readily seen if a plant of the Shepherd's-purse, after washing away the soil, is placed for a day or two with its roots in water (Fig. 2 C, *r.h.*). In the root-system thus treated the extreme tips are seen to be devoid of root-hairs, each being protected by a darker hood-like covering, the *root-cap* (Fig. 2 C, *r.c.*) which is not readily discernible in a freshly uprooted plant. If we scrape the surface of the root with a blunt instrument, we find that the outer part consists of a soft substance, but, if the scraping be continued, we ultimately arrive at a harder central core (Fig. 2 A and B, *c.c.*) which runs the whole length of the root.

We will now turn to a further examination of the aerial part, the shoot. Here again, as in the root, we have to distinguish a vertical main axis (Fig. 1, *a.i.*) bearing lateral branches which, however, grow outwards and upwards. All the lateral branches will be found to arise immediately above a leaf and, since the angle between a leaf and the stem upon which it is borne is termed the *axil* of the leaf (Fig. 3 E, *axil*), the branches are described as axillary (Fig. 1, *ax.b.*, Fig. 3 E, *a.b.*). That part of the stem from which a leaf arises is called a *node* (Fig. 1, *n*), whilst the portion between two nodes is spoken of as an *internode* (Fig. 1, *in.*). At the base of the stem a considerable number of leaves generally arise close together

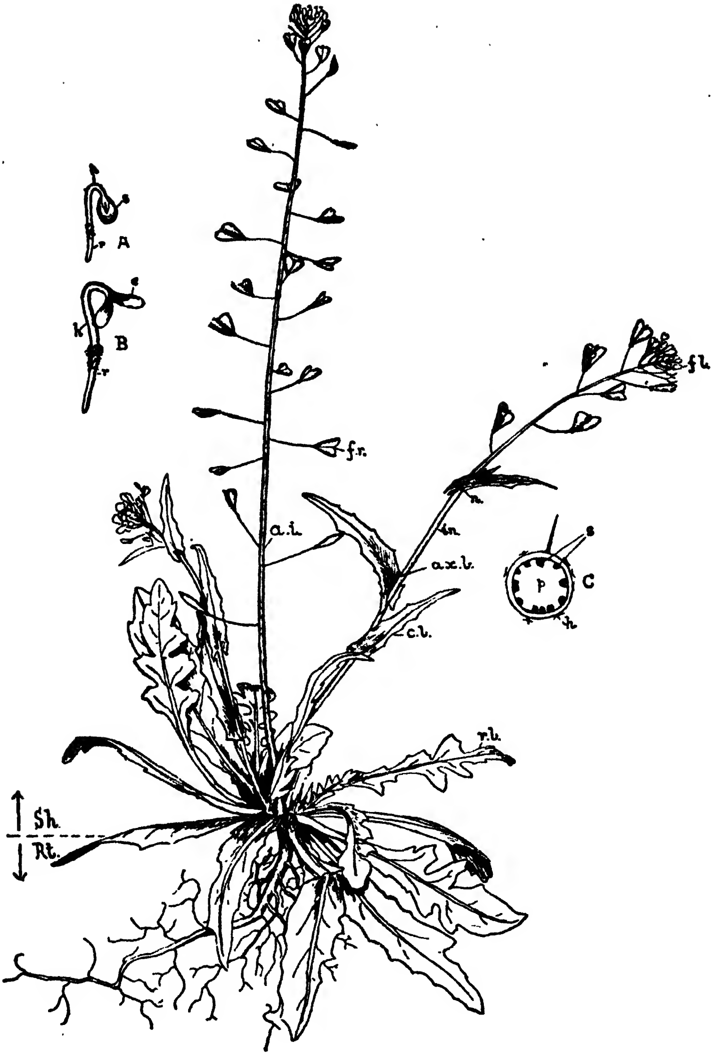

FIG. 1.—Complete plant of Shepherd's-purse (slightly reduced). The surface of the soil is indicated by the dotted line on the left. *a.i.*, axis of inflorescence ; *ax.b.*, axillary bud ; *c.l.*, one of upper leaves ; *fl.*, flowers ; *fr.*, fruit ; *in.*, internode ; *n.*, node ; *r.l.*, leaf of rosette *Rt.*, root ; *Sh.*, shoot. A and B, Two stages in germination (somewhat enlarged). *c*, cotyledon ; *h*, hypocotyl ; *r*, radicle ; *s*, testa C, Cross-section of stem (magnified about 8 diameters). *h*, hair *p*, pith ; *s*, woody strands.

without perceptible internodes, forming a rosette (Fig. 1) on the surface of the ground, though as the plant grows older this rosette tends to die away.

By scraping away the surface of the stem, in the same manner as in the case of the root, we find that the soft outer part is quite a thin layer, and that we almost immediately come to a number of narrow light-coloured threads or strands consisting of harder substance and running lengthwise. On cutting across the stem with a penknife these strands appear as a variable number of pale-green dots (Fig. 1 C, s) situated around the edge of the cross-section, whilst the central region is here

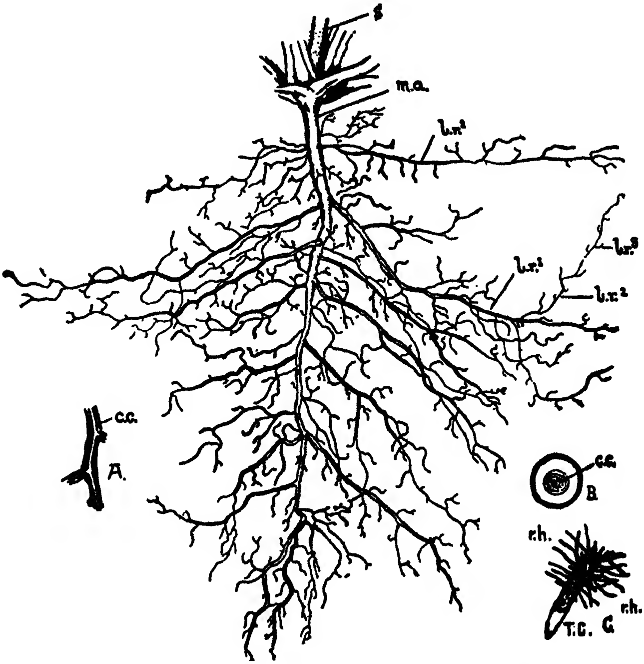

Fig. 2.—Root-system of Shepherd's-purse (natural size). *S*, base of stem; *m.a.*, main axis of root; *l.r.*^{1}, lateral branches of first order; *l.r.*^{2}, laterals of second order; *l.r.*^{3}, laterals of third order. A, Longitudinal section through portion of main root (about 3 times natural size). B, Cross-section of same (× 6); *c.c.*, central core. C, Tip of a root grown in water (× 10). *r.h.*, root-hairs; *r.c.*, root-cap.

occupied by soft tissue (*p*), a marked point of contrast to the root.

In the leaf two parts can usually be distinguished, the leaf-stalk or *petiole* (Fig. 3 B, *pe.*) and the flat part of the leaf, the *blade* or *lamina* (Fig. 3 A, *la.*). The margin of the latter is not regular, but, if we examine a number of plants, all stages from leaves with an almost smooth outline to those in which it is deeply indented can be found (Figs. 1 and 3). In general the upper leaves are less deeply cut and have a shorter leaf-stalk than those forming the rosette—in fact, most of the upper leaves have no petiole and the base of their lamina forms two projections enclasping the stem (Fig. 1, Fig. 3 E). We here encounter a fundamental feature of living organisms, namely, their *variability*. The lamina has one surface directed upwards and the other downwards, and it will be noticed that the upper is darker green than the lower. Extending from the base to

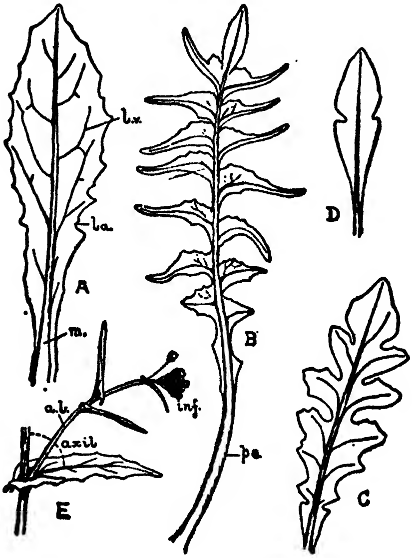

FIG. 3.—A–D, Forms of rosette leaves of Shepherd's-purse (about half natural size). *m*, midrib; *la.*, blade; *l.v.*, lateral vein; *pe.*, petiole. E, Node with leaf and axillary branch bearing inflorescence (*inf.*) (about half natural size). *a.b.*, axillary branch.

the tip of the leaf and forming a direct continuation of the petiole is a prominent strand, which projects markedly on the under side and is known as the *midrib* or principal vein (Fig. 3 A, *m*). Arising from the latter are a number of finer strands (the *lateral veins, l.v.*) which branch still further to form a network (often difficult to see in the Shepherd's-purse) upon which the delicate substance of the leaf is spread out.

The surfaces of stem and leaves bear numerous scattered *hairs* (Fig. 1 C, *h*). These outgrowths are of a white colour, and whilst some, especially prominent on the edges of the leaves, are simple and almost straight, others are branched in a star-shaped manner (Fig. 4 C).

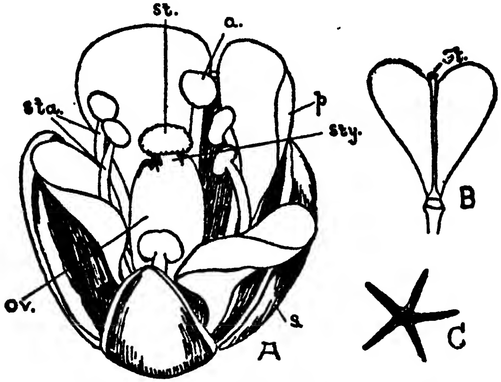

FIG. 4.—A, Single flower of Shepherd's-purse (much enlarged); *s*, sepal; *p*, petal; *sta.*, stamens; *a*, anther; *sty.*, style; *st.*, stigma; *ov.*, ovary. B, Single fruit (much enlarged); *st.*, stigma. C, Single star-shaped hair from leaf (much enlarged).

Terminating the main stem and some of its larger branches are clusters or *inflorescences* consisting of small flowers borne on slender stalks (Fig. 1, *a.i.*; Fig. 3 E, *inf.*). Each flower is composed of the following parts (Fig. 4 A): On the outside there are four small green or slightly purplish leaves, each of which is called a *sepal* (*s*), whilst collectively they are termed the *calyx*; next within, and alternating with the sepals, are four larger white leaves, the *petals* (*p*), together known as the *corolla*; these are followed by six structures called stamens (*sta.*), each of which consists of a short stalk or *filament* bearing at its tip a yellowish swelling or *anther* (*a*) covered with a yellow powder, the *pollen*; in the centre of the flower is situated the *ovary* (*ov.*), which appears as a small, green, flattened structure, surmounted by a short peg-like projection, the *style* (*sty.*), which ends in a little knob, the *stigma* (*st.*).

The pollen of the stamens is received by the stigma and, as a result of further growth, the ovary gradually develops into the ripe fruit (Fig. 4 B), during which the stalk of the flower elongates, calyx, corolla, and stamens wither away, and the internodes between the flowers become drawn out (see Fig. 1). On older plants the ripe fruits are seen, in the lower part of the inflorescence, as flat green triangular structures with an apical notch in which the remains of style and stigma can be distinguished (Fig. 4 B). If we split open a ripe fruit we find inside a number of small pale green bodies attached by short stalks and constituting the seeds; these have developed from minute structures (the *ovules*), present in the ovary of the young flower, as a result of changes following upon the reception of the pollen by the stigma.

Older plants, which have been flowering for some time, will show the ripe fruits opening of themselves and shedding the contained seeds, after which the parent sooner or later dies away. The seeds get washed into the soil by the rain and after a brief period give rise to new plants. In this way the Shepherd's-purse not only reproduces its kind, but also multiplies.

Like most plants, the Shepherd's-purse is built up of innumerable small units called *cells*, the detailed structure of which can only be studied with a microscope. These cells are not all of one kind, differing amongst themselves according to the purposes which they fulfil. At the tips of the branches of root and stem are situated groups of very small tender cells, which during the growing period are constantly multiplying by division into two and thus provide the new units by means of which an increase in length takes place. These groups of cells are consequently termed the *growing points*.

Having thus become acquainted with the general structure of the plant, we may now consider the purposes or functions of its different parts or organs. It is obvious that the root in the first place performs the function of fixing the plant in the soil, as shown by the effort which is often required to uproot it. The efficacy of the root-system in this respect is demonstrated by the difficulty that is experienced, when we attempt to break it, especially by means of a pull; and it will be seen that this is due to the central core of hard substance with which we have already become familiar (p. 2).

In the stem, on the other hand, the woody strands, as we have seen, are situated round the edge (Fig. 1 C), and this arrangement renders the stem more suited to meet bending strains in all directions under the influence of the wind. The leaves which offer a relatively large surface to the wind would of course be particularly liable to become torn, were it not for the fact that the delicate tissue is fully supported by the network of the veins which, with the hard strands of the stem and root, form a continuous skeleton throughout the plant.

The second important function of the root is absorption of water from the soil, a fact which can be simply shown by leaving an uprooted plant lying on the surface of the ground and observing the withering that rapidly ensues. The actual absorption of moisture can be demonstrated by placing a plant of the Shepherd's-purse with its root-system in a tumbler of water, the surface of the latter being covered by a thin layer of oil to prevent evaporation. The level of the water in the tumbler should be marked by a strip of gummed paper, and a perfectly similar arrangement, but without a plant, should be set up beside it to serve as a control. After some hours the level of the water in the tumbler containing the plant will be found to have fallen, whereas no appreciable change is noticed in the control. As we shall learn more fully later on, this absorption of water is actually effected by the root-hairs.

The stem, besides serving to bear the leaves and inflorescences, forms the channel through which the water absorbed by the roots is conveyed to the different parts of the shoot. By cutting off the tips of the roots of a complete plant and placing its root-system in water which is deeply coloured by red ink, the whole course of the water through the plant can be traced. If, after some hours, we split up the main root and stem lengthwise we shall find that the red colour is confined to the hard central core of the root and to the similar strands which run near the surface of the stem. Moreover, the veins of some or all of the leaves (and even parts of the flower) will be seen to be similarly coloured, thus proving that the continuous skeleton referred to above also serves as the water-conveying mechanism of the plant.

The water which is thus brought to the leaves is not pure, but is a very weak solution of certain mineral substances present in the soil, and many of these are necessary for the nourishment of the plant. Of the moisture reaching the leaves a large volume escapes as water-vapour from the extensive evaporating surface which they present, whilst the water retained is built up into the substance of the plant. The continual loss by evaporation is made good by absorption through the roots. A large volume of water is absorbed, but the amount of mineral salts taken in is chiefly dependent on the extent to which they are built up or otherwise altered within the plant's body.

The process of evaporation from the leaves may be roughly studied by using filter paper soaked in a solution of cobalt chloride and subsequently dried in an oven or before a fire. Such paper appears deep blue, but readily turns pink and finally almost colourless on exposure to moisture. Leaves of the Shepherd's-purse are placed on a sheet of dry blotting-paper, some with their upper and some with their under surfaces directed upwards. Small pieces of the dry cobalt-paper are then laid on each, and the entire series is covered with a dry sheet of glass to prevent access of damp air. It will be noticed that the pieces of cobalt-paper in contact with the under surfaces of the leaves become colourless more rapidly than those upon the upper surfaces, thus showing that more water-vapour escapes in a given time from the under than from the upper side.

We shall find later that the surface-skin on both sides of the leaf is perforated by a large number of minute pores which are usually more numerous on the under than the upper surface and whose size varies slightly at different times. The pores are usually wide open in the light and almost closed at night, and it is through them that most of the water-vapour escapes. The rate of water-loss is dependent not only on external, but also on internal, conditions and therefore the process is termed *transpiration*. It is largely the increasing resistance to evaporation of moisture from the internal cells that checks this process, when too little water is supplied by the roots. When almost closed the pores also effectively check evaporation, but in light they usually remain open, even when the plant begins to wither. The reduced transpiration from a wilted as compared with a fresh leaf can be shown with the help of cobalt-paper.

We have already seen that one of the most striking differences between the aerial and underground parts is the green colouration of the former, particularly of the leaves. The colour is due to a mixture of pigments known as *chlorophyll*, which are of importance in the nutrition of the plant. If a plant is killed by immersion in boiling water and is subsequently placed in methylated spirits, a solution of the chlorophyll is obtained, leaving the plant itself colourless. If some of the leaves of the latter are now placed in a solution of Iodine (Appendix I.), they rapidly acquire a bluish-black colour which is a sure test for the presence of starch.

It can easily be shown that starch is only to be found in the leaves after the plant has been exposed for some time to the light. Two similar specimens of the Shepherd's-purse should be planted in separate pots and, whilst one is left exposed, the other is covered over so as to be in darkness. After forty-eight hours a leaf is removed from each plant and decolourised in the way described above. On treatment with Iodine it will be found that the starch-reaction is only shown by the leaf from the exposed plant. We thus see that starch-formation in the leaves goes on only in the presence of light.

If the experiment we have just performed be continued for several weeks, the plant in the dark assumes a starved appearance as compared with the one in the light, so that starch is evidently an important food-substance. It will also be noticed that any new leaves formed in the dark are practically colourless, which shows that light is necessary for the formation of chlorophyll. If such a plant is subsequently exposed to illumination, it will be found that starch soon reappears in the green leaves, but no starch is produced in the colourless leaves until after they have become green. This proves that chlorophyll also is necessary for starch-production.

It will subsequently become apparent that the starch in the leaves of plants is formed, with the help of light and chlorophyll, from the carbonic acid gas (or carbon dioxide) of the air and some of the water which passes into the leaves, the air obtaining access to the interior through the pores above mentioned. During this process Oxygen is given off. The necessity of carbonic acid gas for the production of starch can be shown by the following experiment.

Two plants of the Shepherd's-purse in pots are kept in the dark until a leaf from each gives no starch-reaction with Iodine. One of the plants is placed upon a glass plate, and soda-lime (Fig. 5, *S.L.*), which absorbs carbon dioxide, is heaped up around the lower part of the pot, the whole being then covered by a bell-jar, whose edge has been previously vaselined to form an air-tight connection (Fig. 5). The second plant, serving as a control, is similarly treated, but no soda-lime is placed beneath the bell-jar, and both experiments are then exposed to bright sunlight. After some hours a leaf is removed from each plant and tested for starch, whereupon it will be found that the one under the bell-jar containing the soda-lime has failed to form starch owing to the absence of carbonic acid gas.

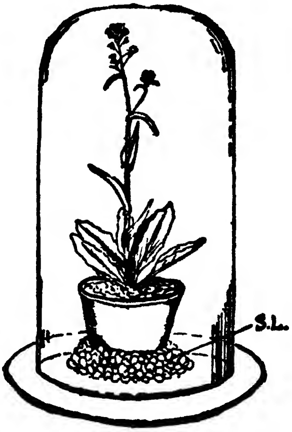

Fig. 5.—Apparatus to demonstrate that a Shepherd's-purse plant does not form starch in the absence of carbon dioxide. *S.L.*, soda-lime.

The building up of starch and other carbohydrates from carbon dioxide and water is spoken of as ***carbon dioxide assimilation***, and, owing to the part which light plays in the process, the alternative term *photosynthesis* is often employed. This is the first step in the nutrition of the plant and leads on to the formation of the more complicated proteins of which it largely consists and in the production of which the mineral salts absorbed from the soil play a part.

There remains one other important vital process carried on by the plant, viz. the taking in of Oxygen and the giving out of carbon dioxide. This is the breathing process (*respiration*) common to plants and animals. The exchange of gases in this case is just the reverse of what occurs in assimilation, and this latter being a much more active process, respiration is completely masked in the presence of light. Consequently a satisfactory demonstration of the fact that plants breathe can only be obtained in the dark. To demonstrate the need for Oxygen, soaked Peas are placed in a U-tube, one end of which is closed by a rubber-cork. The U-tube is then inverted with the Peas resting on the cork and the other end is placed dipping in a solution of pyrogallate of potash (Appendix IX). The exposed surface of the solution is at once covered with oil. In the control, water is used to replace the pyrogallate. Whereas the Peas in the control sprout, those in the other apparatus fail to do so, which we may attribute to the pyrogallate having absorbed all the Oxygen from the air within the tube. Breathing, in fact, is just as essential for the existence of the plant as for that of the animal.

The substances requisite for the nourishment of the plant are thus obtained from two sources, viz. the soil and the air. The root fixes the plant in the ground and absorbs water which contains mineral salts in solution. Most of this water is given off in transpiration, but the remainder, together with the dissolved salts, is retained and contributes to the maintenance of the plant. Through the agency of the chlorophyll in the presence of light chemical changes are brought about, which transform the carbon dioxide and some of the water into food-substances. These together with their further products not only serve for the nourishment of the plant, but supply the material for continued growth. In this way the seedling, living at first on food stored within the seed, is able to increase in size and finally to form fresh seeds, capable of giving rise to a new individual. All of these vital processes involve a loss of energy, made good by the energy set free in respiration, and hence its importance for the maintenance of life.

The outline above given of the life of a green plant emphasises several prominent distinctions between the Vegetable and Animal Kingdoms. Of these the most striking is the difference in the mode of nutrition. The plant takes in simple chemical substances in the form of solutions or gases which, with the help of the energy of the sun's light, are built up into food. On the other hand, most animals take in solid nourishment, consisting not of simple chemical substances, but of complex organic compounds (carbohydrates, fats, proteins), which they have obtained second-hand, either directly from the Vegetable Kingdom or indirectly (in the case of Carnivores) from other herbivorous animals. So that, if green plants were to disappear from the surface of the earth, almost the whole organic world would shortly perish.

In the breathing process, however, there is no fundamental difference between the two Kingdoms. In both cases there is an absorption of Oxygen, which effects oxydation of complex compounds within the organism and liberates energy, just as energy is set free in the form of light and heat during the burning of a candle. Since animals exhibit greater activity than plants, their consumption of energy is greater and their breathing more rapid. The energy liberated by the plant in respiration is a small fraction of that present in a latent state in the compounds built up during photosynthesis, whilst that set free in the breathing of animals is likewise solar energy, latent in compounds which owed their origin to plants, and have entered the animal body as food.

Plants as a whole are essentially sedentary (*i.e.* rooted to one spot) and animals essentially motile. This distinction may be related to the necessity for most animals to move from place to place in search of food, whilst plants, depending as they do almost solely on simple chemical compounds, can best obtain these by being stationary. It will, for instance, be clear that, for the terrestrial plant, the intimate contact which is necessary between root and soil is totally inconsistent with a motile habit. Another distinction between higher plants and animals is the possession by the latter of highly-developed sense-organs. This, too, can probably be related to the motile habit, with the concomitant necessity for rapid response to the everchanging environment. It is significant that in animals like the Hydrazoon *Obelia*, which have a motile and sedentary phase in their life-history, the more specialised organs of sense occur in the former.

During its life the ordinary plant exhibits a constant production of new organs (leaves, flowers, etc.) wherein it differs markedly from the average animal. A further point of distinction lies in the fact that in those plants that live for more than one year, only a part of the body usually persists from season to season. (Cf. the next chapter.)

CHAPTER II

PLANT-HABIT AND DURATION

A NUMBER of our common plants, such as the Poppy, the Sweet-pea, and the Nasturtium, appear above ground in the early spring, arising from seeds that have lain dormant in the soil during the winter. After a period of rapid growth flowers are formed and these, towards the end of the season, produce fruits from which the seeds are eventually shed; subsequently the rest of the plant dies away, and the same sequence is repeated in the following seasons. Such plants, which pass through the whole of their life-history in the course of a single year, are called *annuals*. There are some plants, particularly weeds like the Shepherd's-purse (Fig. 1) and the Groundsel, in which the whole life-cycle occupies a much shorter interval of time, so that several successive generations are produced in the same year. Owing to their rapid growth such plants, which are termed *ephemerals*, readily establish themselves on new ground.

The annual uses up all of its available food-materials in the production of seeds, but if this be prevented by removing the flower-buds as they appear, it may in many cases be induced to survive into a second season. There are, however, a large number of plants which normally in nature require more than a single year to amass the necessary food-materials for seed-formation. Some of these, which are termed *biennials*, flower only in the second year of their life and soon afterwards die away; examples are furnished by the Mullein (Fig. 6), Canterbury Bell and the Carrot. Such plants during the first season's growth do not get beyond the production of a rosette of leaves close to the surface of the ground (Fig. 6 B). The food-substances formed by these leaves pass into the subterranean portion, which becomes swollen and serves as a storage-organ (Fig. 20 A, p. 42). During the ensuing winter the plant remains in a dormant condition, the leaves, since they lie in close proximity to the soil, obtaining a certain amount of protection by surrounding vegetation and inequalities of the surface of the ground. In the following year rapid growth takes place, largely at the expense of the food stored up in the underground parts, and as a result a tall stem bearing a mass of flowers is produced (Fig. 6 A). Under certain circumstances, such as growth on very poor soil, the biennial will be found to form a few flowers and seeds already in the first year and then to die away, thus behaving like an annual.

Fig. 6.—The Mullein, a biennial (greatly reduced). B, In the rosette-stage (first year). A, In the stage found in the second year.

We can readily imagine a biennial in which the vitality of the plant is not completely exhausted by the production of flowers and fruits, so that sufficient food-material remains to support renewed growth in the following spring. If this goes on from year to year we should obtain a so-called *perennial*, and a large number of plants in nature persist in this manner. As instances we may mention the Stinging-nettle, the Dog's-mercury, the Perennial Sunflower, the Crocus, the Iris, and the Solomon's Seal. If such plants are grown from seed, some will be found to flower already in the first year, whilst most require two or even more years to attain to sufficient vigour before flowers are produced; meanwhile they are accumulating a store of food in their underground organs (cf. Fig. 20, B of the Lesser Celandine).

In the examples above mentioned the aerial parts die down at the end of each season, whilst the subterranean parts (the bulb in the case of the Tulip, the stem in the Solomon's Seal) persist and by virtue of their store of food-material rapidly produce new shoots in the following spring. When the plant begins to form flowers, it is sufficiently vigorous to provide the necessary food for the resulting seeds, and yet to transfer enough into the underground organs for the commencement of next year's growth. A few perennials of the type we are considering, such as the Dandelion or Iris, always retain some of their leaves even during the winter, although in other respects they behave exactly like those we have described.

The kinds of perennials hitherto noticed are called herbaceous perennials, since they produce no permanent overground shoot-system. In contrast to these, however, a large number of perennials, namely shrubs and trees, form stems which become hard and woody and consequently persist to form the starting-point for each year's growth, a feature that enables them to attain in many cases to very considerable dimensions. In the British flora such *woody perennials* are confined to one of the two great subdivisions of flowering plants, the so-called Dicotyledons (cf. p. 31), although this habit is also found among the Conifers (*e.g.* Scotch Fir, Yew, etc.). Even in these forms some part, as a general rule, dies back on the approach of winter, as is seen in the falling of the leaves of plants like the Beech, Oak, Briar, Hawthorn, etc., which are consequently described as *deciduous*. A few others, such as the Holly and the Scotch Fir, are *evergreen*, bearing leaves at all times of the year.

The store of food in these woody perennials is laid down throughout the woody portion of the plant and is here again responsible for the rapid sprouting which takes place with the advent of spring. Trees and shrubs, the two kinds of woody perennials, are distinguished by the fact that the former have a prominent main trunk on which the smaller branches are borne, whilst shrubs have a number of nearly equal main stems arising side by side.

The form of food-reserve in perennial plants is commonly starch, a fact which may be easily verified by cutting open the underground stem of the Iris or Crocus or a thick branch of the Horse Chestnut in winter, and applying the Iodine-test (see p. 10). In other cases (*e.g.* the Solomon's Seal and the Dandelion) forms of food-material not giving this reaction are found, but a further consideration of these must be deferred till later.

The fact that so many plants die back on the approach of winter suggests that this may be related to the commencement of colder weather. During winter the temperature of the soil is often so low that absorption of water by the roots practically ceases. If, under these circumstances, the plant were to lose water in transpiration (p. 9) at the same rate as in the warmer period of the year, it would soon wither and die. This evil is, however, avoided by the shedding of the leaves or the dying away of the whole overground shoot-system whereby the transpiring surface is reduced as much as possible. At first sight the evergreen would appear to be an exception to this rule, but it will be noticed that all evergreen leaves (*e.g.* the Laurel and the Holly) are of a leathery texture, due to an unusually thick surface-skin. As a consequence, transpiration from such leaves goes on slowly at all times of the year, and such little absorption as occurs during the winter is sufficient to replace this loss. It is instructive in this connection to compare the relative rates of transpiration of a deciduous and an evergreen leaf by the aid of the cobalt-method (p. 9).

Plants exhibit a number of diverse habits, of which the erect is by far the most frequent ; in this type the aerial shoot-system is so constructed as to be able to support itself, and examples are furnished by all the plants we have as yet mentioned. It is natural to ask why these plants constantly assume the erect position in nature, and the question may be answered in the following way. If an erect plant be placed next to a window, so that it receives one-sided illumination, the shoot will soon be found to have curved over towards the light (Fig. 7 B). When this has occurred the plant should be turned round through half a circle, whereupon after a further interval the shoot will again bend over towards the window. We thus see that the erect growth of the stem is dependent on its being exposed to equal illumination on all sides, and that one-sided light causes a bending until this state of affairs is attained. The influence of light upon the direction of growth of the plant is spoken of as *heliotropism.*

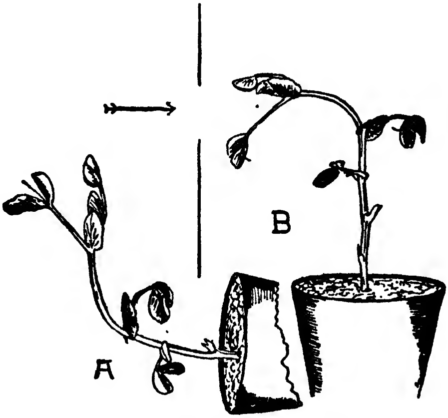

Fig. 7.—A, Seedling of Pea, placed horizontally in the dark, showing the shoot bending up under the influence of gravity. B, Ditto, placed vertically and showing a heliotropic curvature under the influence of one-sided light, whose direction is indicated by the arrow. (About one-third natural size.)

It is not difficult to show that other influences play a part in determining the erect position of the shoot, for if we place a potted plant horizontally in the dark for some hours the tip of the shoot gradually curves upwards till it again assumes a vertical direction (Fig. 7 A); the same thing may be frequently observed in nature, when a plant without being uprooted is blown over by the wind, or a branch sinks down as a result of its own weight. In the plant placed in darkness some agency other than light is evidently at work, and, as we shall only be able to understand fully later on, this is the force of gravity which in this case has the peculiar effect of causing growth in a direction opposite to that in which gravity acts. The influence of this force on the direction of growth of the plant is termed *geotropism*.

FIG. 8.—Photograph of foot of hedge-row, taken close at hand. *b*, White Bryony ; *c*, Chickweed ; *g*, Goose-grass ; *p*, Beaked-parsley ; *s*, Stinging Nettle.

A few plants, like the Ground Ivy, possess creeping stems, whilst in some the upright shoots are so weak that they have to rely on the support of others in order to expose their leaves and flowers to the air and light. In this habit they are aided by twining stems (Convolvulus, Honeysuckle), hooks (*e.g.* Briar, Goose-grass, Fig. 8), rootlets (*e.g.* Ivy), or special thread-like developments of the leaves or branches known as tendrils (*e.g.* Sweet Pea, White Bryony, Fig. 98). Such climbers economise the material which ordinary plants have to employ in the formation of their supporting skeleton, and as a consequence exhibit exceptionally rapid growth.

Not infrequently one particular type of habit is especially characteristic of certain situations. Thus, the plants of a heath or moorland mostly possess small leaves, often of a leathery texture, whilst by contrast the herbs of a woodland have large thin leaf-blades. Climbers are most frequent in hedge-banks (Fig. 8) and wood-margins; whilst succulents, such as Cacti and the Stonecrop, are principally met with in dry places. Each type of growth has its own advantages in relation to the conditions which obtain in the situation where it characteristically occurs.

CHAPTER III

Dicotyledonous Seeds and Seedlings

We have seen that, as in the Shepherd's-purse, most flowering plants sooner or later in the course of their life produce fruits and seeds which represent the culmination of each season's growth. Having become detached from the parent-plant in one way or another, the seeds eventually come to lie on the rugged surface of the soil. By the action of the summer's heat and winter's frost the soil becomes broken up, and into the numerous cracks and crevices thus formed the seeds find their way. Burrowing animals, especially Earthworms, contribute to this process of disintegration and, since in the course of their nutrition considerable quantities of soil are passed through their bodies and become deposited at the surface, they constantly transfer earth from below upwards. In rainy weather the little streams of water that percolate into the ground wash the seeds still deeper, whilst at the end of each season's growth fallen leaves and other vegetable *débris* accumulate on the top of the soil and thus afford added protection to the seeds below. In these various ways the seeds become buried at some slight depth in the soil.

In many plants the seeds remain dormant in the ground until the following spring, when conditions become favourable for their sprouting or *germination*. It is easy to show that seeds only germinate when provided with sufficient moisture, warmth, and adequate Oxygen for breathing (cf. p. 12). The effect of moisture can be demonstrated by planting seeds of the same kind in half a dozen small (3 in.) pots filled with dry soil or sawdust; the first pot receives no water, the second is given a small amount (*e.g.* 3 c.c.) each day, the third double as much as the second, and the remainder in correspondingly increasing amounts, so that the last pot receives daily 48 c.c. It will be found that the seeds in the first three pots either fail to germinate or do so (in the case of the third) only after a long interval, whilst those in the fourth and fifth soon begin to grow. The seeds in the last pot may in some cases be found not to germinate so rapidly as those in the preceding two, which is due to the large quantity of water added displacing the air from the spaces between the particles of the sawdust or soil, so that respiration is hindered.

In nature, the supply of water and Oxygen are as a rule sufficient for the germination of seeds, and it is the low temperature of the soil that delays this process until the spring. If soaked seeds are planted in three pots of sawdust, one being placed in a cold room (or in summer surrounded by ice), the second in a moderately warm room, and the third about a yard from a fire or radiator, all being sufficiently watered, it will be found that the higher the temperature the more rapidly does germination ensue.[1] Most seeds, however, even if placed under suitable conditions, will not germinate immediately after being shed, but require a longer or shorter period of rest.

Dormancy in seeds is a phenomenon dependent on various causes, of which the commonest is probably the difficulty with which water penetrates the coat of the seed. In many seeds with comparatively impermeable coats, such as Sweet Peas or Lupines, abrasion of the latter will hasten germination.

We may now study the outward characters of some common seed such as that of the Runner Bean (Fig. 9 A). We notice that it is more or less kidney-shaped and is covered with a smooth, tough skin, the seed-coat or *testa*. Along the middle of one of the long edges of the seed there is a narrow white scar (the ***hilum, h***) which marks the point at which the seed was attached to the pod. At one end of the hilum are two minute swellings (*s*) side by side, whilst near the opposite end is a very small hole (the ***micropyle, m***) situated at the base of a slight depression.

When such seeds are soaked in water, the liquid is absorbed through the micropyle, and gradually the seed-contents swell up so as finally to burst the testa. If the latter be now removed,

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[1] The seeds placed on ice will probably not germinate at all.

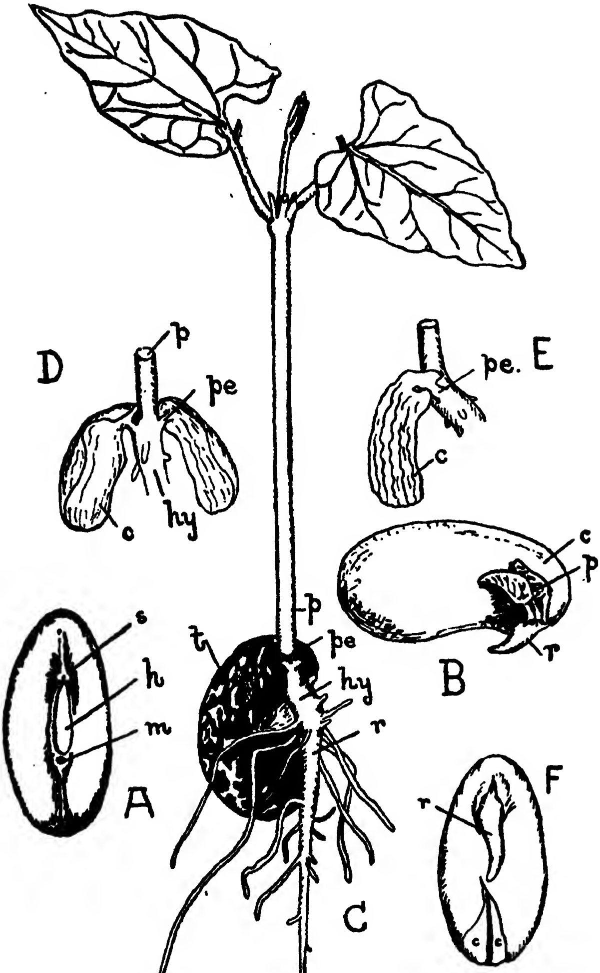

FIG. 9.—Stages in the germination of the Runner Bean (all natural size). A, Soaked seed seen edge on, to show the hilum (*h*), the micropyle (*m*), and the swellings (*s*). B, Seed with testa and one cotyledon removed to show plumule and radicle. C, Mature seedling. D, Partially shrivelled cotyledons, showing attachment to base of plumule. E, Ditto from side, with completely shrivelled cotyledon. F, First stage in germination. *c*, cotyledon ; *hy.*, hypocotyl ; *p*, plumule ; *pe.*, stalk of cotyledon ; *r*, radicle ; *t*, testa.

two cream-coloured fleshy lobes, the seed-leaves or *cotyledons*, are disclosed (Fig. 9 B, *c*). If the cotyledons be carefully separated, a small bud bearing minute yellowish-green leaves (the *plumule* or primary shoot, Fig. 9 B, *p*) will be seen lying between them near to one edge. A close scrutiny shows that each cotyledon is attached to the base of the plumule by a very short stalk, whilst beyond this point the axis of the plumule is prolonged into a short tapering outgrowth, the *radicle* or primary root (*r*). Whereas the plumule is completely hidden between the cotyledons, the radicle after removal of the testa is seen as a projection lying against their edges (cf. Fig. 9 B). The young plant, which we have thus found within the seed, is termed the *embryo* and includes three types of organs, viz. the radicle, plumule and cotyledons.

It will be noticed that the tip of the radicle fits into a short pocket which arises from the inner surface of the seed-coat and ends near the micropyle. This pocket acts like the wick of a lamp in drawing up moisture from the soil and passing it on to the radicle, so that this is the first part of the embryo to receive water and swell to a considerable size. As a result it is here that the pressure upon the seed-coat is most pronounced and that the bursting of the testa begins. The radicle, thus freed, grows rapidly downwards (Fig. 9 F) and very soon side-roots arise from it, so that the young plant becomes firmly anchored in the soil. In the meantime the stalks of the cotyledons are slowly increasing in length (Fig. 9 D, *pe*) and, since the cotyledons themselves remain firmly embedded in the seed on the one hand and the root is fixed in the soil on the other, this elongation has the effect of carrying out the plumule clear of the seed-coat (Fig. 12 A). Up to this time the plumule has altered little in size, but now a rapid growth in the upward direction begins. It will be seen that, until after the surface of the soil is reached, the tip of the plumule remains sharply curved, so that it is the more mature region that pushes its way through the ground, dragging after it the young tender leaves at the apex, for which a passage is thus created. This curvature rapidly straightens out after the plumule comes above the surface of the soil into the light (Fig. 9 C).

The early stages of germination are accomplished in darkness, and as a consequence the seedling is unable to manufacture starch and similar food-materials (cf. p. 10). As a matter of fact the early growth of the embryo takes place at the expense of food-substances which became stored up within its cotyledons, whilst the seed was still attached to the parent-plant. The bulk of this food consists of starch, and its presence can therefore be demonstrated by breaking across a cotyledon and applying Iodine to the exposed surface. If seedlings are examined at successive stages of germination, it will be seen that, as growth proceeds, the cotyledons shrivel up more and more (Fig. 9 D and E) until finally but a shrunken remnant is left. It will thus be apparent that in the Runner Bean the cotyledons are merely storehouses for nourishment and never come above the soil, though, as other examples will show, they do not always behave in this way.

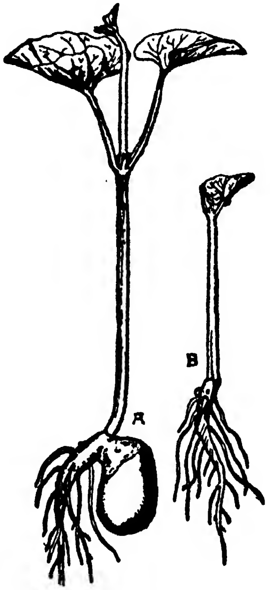

FIG. 10.—A, Normal seedling of the Runner Bean. B, Seedling of the same age, from which the cotyledons were removed at an early stage of germination. (Both about half the natural size.)

An experimental demonstration of the great part played by the food-reserves in early stages of germination is furnished by cutting off the cotyledons from a number of seeds in which the radicles have obtained a hold upon the soil, care being taken not to injure the remaining part of the embryo in any way. A comparison of normal seedlings with those from which the cotyledons have been removed will show how great an asset this store of nourishment is to the plant (Fig. 10).

As a second example of a seed we may take that of the Castor Oil plant (Fig. 11 A). Neither the hilum nor the micropyle are visible on the testa (*t*) in this case, owing to their being covered by a pale warty outgrowth (*car.*), which arises late in the development of the seed. By splitting the latter lengthwise in the plane of flattening and examining the exposed surfaces of the two halves a thin white leaf-like structure showing midrib and lateral veins will be seen on each (Fig. 11 B, *c*). These are the cotyledons, which in this case are very thin and only occupy a small portion of the seed-contents (Fig. 11 C, *c*). On one half or the other, at the narrower end of the seed, will be found a small white peg (Fig. 11 B), the pointed end of which lies nearest the outgrowth and constitutes the radicle (*r*), whilst the opposite blunt end represents the plumule (*p*). The stalks joining the cotyledons to the base of the plumule are in this case so short as to be hardly recognisable.

We thus see that the embryo of the Castor Oil seed, while showing the same organs as that of the Bean, is much less developed in the resting condition. A further distinction lies in the fact that the embryo of the Castor Oil only occupies part of the seed and that it is completely surrounded by a white fleshy mass, the *endosperm* (Fig. 11 B and C, *e*), which is all that one sees when the seed-coat is removed. This is a tissue containing food-reserves for the nourishment of the young plant, and the chief difference from the Bean is therefore that in the latter the food-substances are stored up *in the embryo itself*, whereas in the Castor Oil there is this special food-tissue *outside the embryo*. Since the endosperm is sometimes spoken of as the albumen, seeds which possess this tissue are said to be *albuminous*, whilst those lacking it (*e.g.* the Bean) are described as *exalbuminous*. Treatment of a broken surface

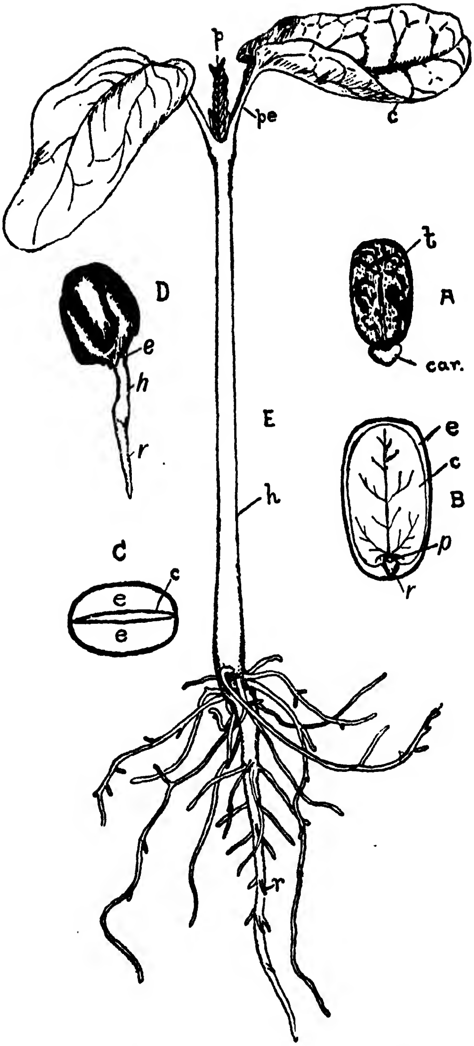

FIG. 11.—Structure of seed and germination of Castor Oil plant (A, D and E natural size, the others enlarged). A, Entire seed. B, The same halved lengthwise. C, Ditto, cut across. D, First stage in germination. E, Mature seedling. *c*, cotyledon ; *car.*, outgrowth ; *e*, endosperm ; *h*, hypocotyl ; *p*, plumule ; *pe.*, petiole of cotyledon ; *r*, radicle ; *t*, testa.

with Iodine will show that starch is not present in the endosperm of the Castor Oil seed, its place being taken by the oil which is used medicinally (cf. p. 100).

The first result of placing seeds of the Castor Oil to soak is that the outgrowth which sucks up water like a sponge increases in size and becomes softer. The seed-coat in this case is so rigid that practically no swelling of the seed as a whole is observed, and, since the water absorbed by the outgrowth is passed on to the adjacent radicle, this part of the embryo is again the first to swell up, leading to a rupture of the testa at this point. The radicle grows downwards into the soil (Fig. 11 D) and begins to form lateral roots whereby, as in the case of the Bean, the young plant becomes fixed. If a slightly older seedling is examined (Fig. 12 B), it will be noticed that prominent elongation is taking place in a region of the axis situated between the place of origin of the lateral roots and the point of attachment of the cotyledonary stalks. This elongating region has a reddish tinge in contrast to the white root and represents a portion of the stem situated *below* the cotyledons, for which reason it is spoken of as the *hypocotyl* (Fig. 12 B, *h*). Such a hypocotyl is present also in the Runner Bean (Fig. 9 D, *hy*), but remains so short that it is difficult to recognise.

The rapid growth of the hypocotyl in the Castor Oil results in its becoming arched upwards (Fig. 12 B), and very soon the top of this arch appears as a loop above the surface of the soil. Subsequent to this the hypocotyl begins to straighten as a result of its further growth, and consequently the cotyledons with the plumule enclosed between them are dragged out of the ground (Fig. 11 E).

If a seed be examined a little time before the cotyledons emerge, the endosperm will be found to have nearly disappeared. During their long sojourn beneath the surface the cotyledons are occupied in absorbing food from the endosperm for the growth of the seedling, and throughout this period are undergoing a great increase in size, so that when they come above the ground they are many times larger than in the resting seed and have pronounced petioles (Fig. 11 E, *pe*). As the hypocotyl becomes erect the cotyledons spread out their blades (which have meanwhile developed chlorophyll) to the light (Fig. 11 E), and now serve as assimilatory organs for the young plant; subsequently by the growth of the plumule other leaves develop to take their place and the cotyledons drop off.

The method of liberation of the plumule from the seed is obviously quite different in the two cases we have studied (cf. Fig. 12), for, whilst in the Runner Bean this is effected by elongation of the cotyledonary stalks, in the Castor Oil it is the lengthening of the hypocotyl that fulfils this purpose. In both cases the delicate tip of the plumule does not push its own way through the soil, this being accomplished either by the older part of the plumule or by the hypocotyl; in the case of the Castor Oil the risk of injury by friction with the soil-particles is still further reduced owing to the inclusion of the plumule between the cotyledons during its passage through the ground. Another difference between Runner Bean and Castor Oil lies in the behaviour of the cotyledons, since in the former they remain permanently underground and are said to be *hypogeal*, whilst

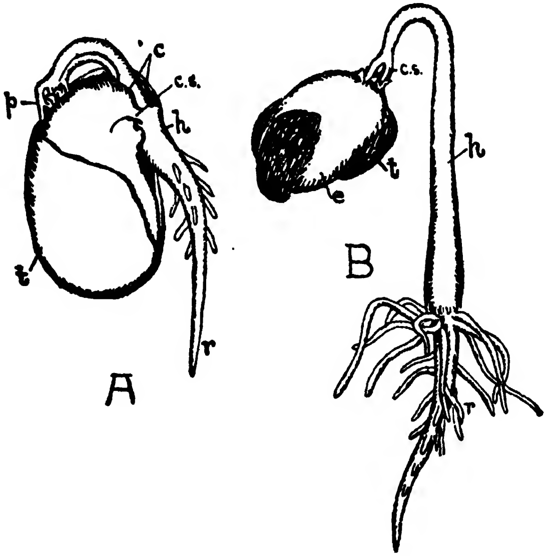

Fig. 12.—Liberation of plumule in A, the Runner Bean; B, the Castor Oil (about natural size). *c*, cotyledons; *c.s.*, cotyledon-stalk; *e*, endosperm; *h*, hypocotyl; *p*, tip of plumule; *r*, radicle; *t*, testa.

in the latter case they eventually appear above the surface and are described as *epigeal.* It may be well to draw attention to the fact that there are also exalbuminous seeds with epigeal cotyledons, as, for instance, the French or Kidney Bean and the Shepherd's-purse (Fig. 1 A and B).

The two types of seed-structure and germination so far described are characteristic of a large number of flowering plants which, owing in part to their possession of embryos with two cotyledons, are grouped together under the name of Dicotyledons. The Grasses, Lilies, and their allies, on the other hand, have but one cotyledon, and for this and other reasons are placed in a distinct group known as Monocotyledons. Apart from the difference in the number of cotyledons, however, the embryo of Monocotyledons shows the same essential organs as that of Dicotyledons.

A monocotyledonous embryo is easily examined in the grain of the Maize (Fig. 13, A). On one of the flat faces a whitish oval depression marks the position of the embryo (*e*), the remaining yellow part of the contents of the grain consisting of endosperm. If the envelope is carefully removed from a soaked grain a somewhat darker line is seen to run vertically up the face of the exposed embryo. By cutting a shallow slit along this line with the extreme point of a penknife and turning back the two edges of the cotyledon thus obtained (Fig. 13 B), two peg-like projections are exposed, one directed towards the original point of attachment of the grain and representing the radicle (*R.S.*), the other placed in the opposite direction and constituting the plumule (*P*). The remainder of the white embryo comprises the single large cotyledon (*c*) which, as we have seen, is wrapped round both plumule and radicle (cf. Fig. 13 F). A further insight into the structure of the embryo is obtained by halving the peeled grain lengthwise along the same dark line as before (cf. Fig. 13 I).

The radicle is again the first part of the embryo to receive water and the first to emerge, bursting through the skin of the grain and growing down into the soil (Fig. 13 E). The appearance of the radicle is very soon followed by the outgrowth of the plumule, which in this case pierces the skin by its ***own active growth*** and, remaining straight, pushes its way to the surface (Fig. 13 C and D). Soon after, the inner leaves of the plumule

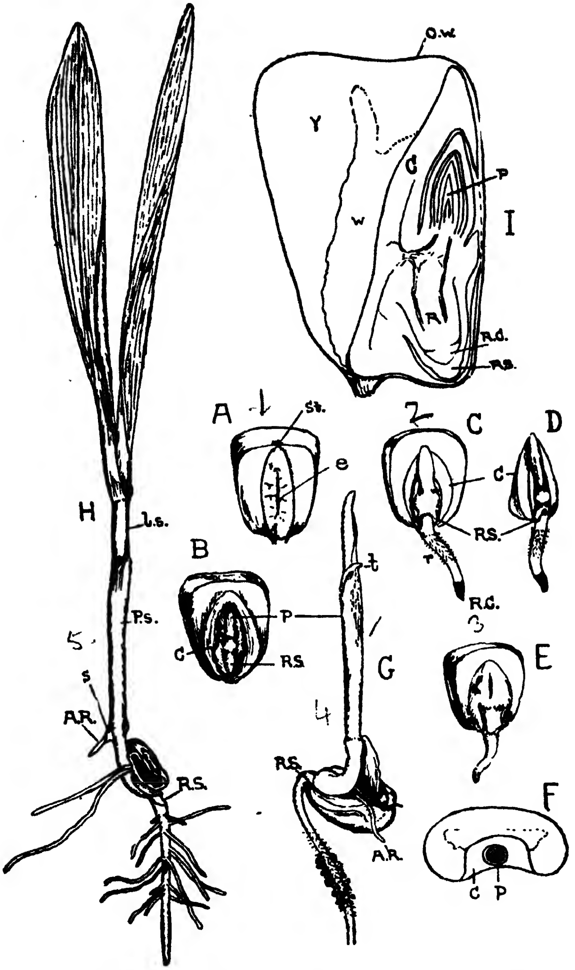

FIG. 15.—Structure of grain and germination in the Maize (all figures slightly enlarged, I ×8). A, Entire grain showing outline of embryo. B, Grain with envelope removed and edges of cotyledon folded back to show plumule and radicle. C, Early stage in germination, envelope removed. D, Embryo of same, dissected out. E, First stage in germination. F, Cross-section of grain with envelope removed. G, Late stage in germination showing escape of foliage-leaves from sheath. H, Mature seedling. I, Longitudinal section of complete grain (much enlarged). *A.R.* (in G and H), secondary roots; *c*, cotyledon; *e*, embryo; *l.s.*, leaf-sheath; *O.W.*, ovary-wall; *P*, plumule; *P.s.*, plumular sheath; *R*, radicle; *R.C.*, root-cap; *R.S.*, root-sheath; *S*, sheath round base of secondary roots; *st*, stigma; *t*, tip of plumular sheath; *W*, starchy endosperm; *Y*, hard endosperm.

begin to grow rapidly, and, bursting the outermost sheath, become exposed to the light (Fig. 13 G and H). Simultaneously several secondary roots (Fig. 13 G and H, *A.R.*) grow out from the base of the stem and aid the radicle in anchoring the young seedling.

During the whole process of germination the cotyledon remains underground within the seed, and is actively absorbing nourishment for the growing embryo from the adjacent endosperm. When examining the grain it will have been noticed that two regions are distinguishable in the latter, the portion nearest the embryo being white and relatively soft, whilst the remainder is yellow and harder (Fig. 13 I, *W* and *Y*). If we halve a grain lengthwise and treat the cut surface with iodine, it will be found that the white portion alone gives the starch-reaction.

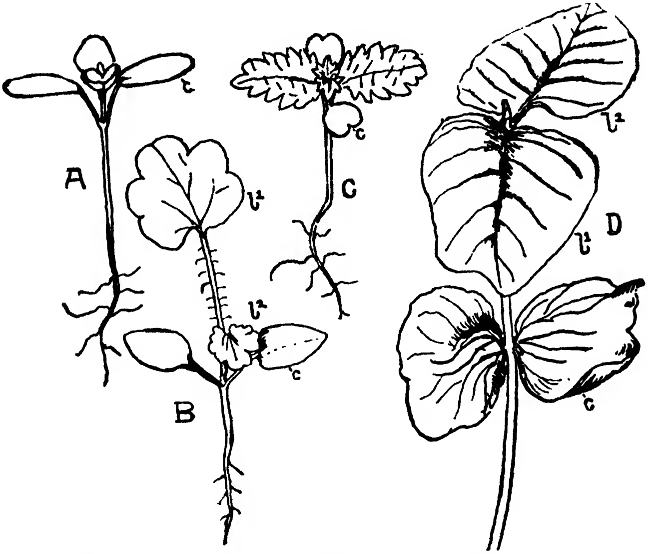

FIG. 14.—Different types of Dicotyledonous seedlings (all natural size). A, Garden Spurge. B, Greater Celandine. C, Stinging Nettle. D, Beech. *c*, cotyledons ; l^1 and l^2, first and second foliage-leaves.

The first result of the absorption of water in germination is thus in all cases the escape of the radicle, and in many seeds its penetration into the soil is aided by devices for fixing the seeds (*e.g.* slimy seed-coats, as in the Cress). The culmination of the process of germination is the liberation of the plumule, which may be effected in various ways, viz. by elongation of the stalks of the cotyledons (Bean), by elongation of the hypocotyl (Castor Oil), and by its own direct growth (Grasses).

Cotyledons either serve directly as storage-organs or as a means of transference of the food-material from the endosperm. In either case they may shrivel up after these purposes are fulfilled, or they may subsequently appear above the ground and function for a time as organs of assimilation. Such epigeal cotyledons are always simple in form and among Dicotyledonous plants usually differ to a more or less marked extent from the subsequent foliage-leaves, as will be quite apparent from a consultation of Fig. 14. In many cases the leaves immediately following on the cotyledons have a simpler form than those developed later, and this is especially marked in plants whose mature leaves are deeply divided (*e.g.* the Ash and the Greater Celandine, Fig. 14 B). The foliage in such cases exhibits a progressive increase in complexity as the plant grows older.

CHAPTER IV

THE ROOT AND ITS FUNCTIONS

WE have seen in the first chapter that the two chief functions of the root are attachment to the soil and absorption of water, and we may now obtain a further insight into the suitability of the root for these purposes. If the root of a young Bean- or Pea-seedling (Fig. 15) is examined, we can distinguish, as in the Shepherd's-purse, root-cap (*r.c.*), root-hairs (*r.h.*) and lateral roots (cf. Fig. 9 of the Bean). The two former are again best seen if the seedlings have been kept for two or three days in water.

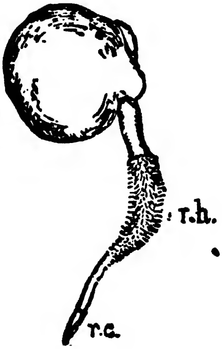

FIG. 15.—Young Pea-seedling with radicle showing root-hairs (*r.h.*) and root-cap (*r.c.*) (about twice natural size).

The root-cap serves the purpose of protecting the delicate cells of the growing point at the tip of the root from injury whilst the latter is forcing a passage through the soil. During the elongation of the root the outer surface of the cap gradually breaks down and becomes slimy, so that the root-tip glides easily between the particles of earth. As the substance of the root-cap wears away in front, new tissue is continually formed from the growing point behind, and thus the cap remains of almost constant thickness.

It will be noticed that there is a varying extent of bare root between the apex and the region occupied by the root-hairs (Fig. 15). It is in this region, and here only, that increase in length is taking place in the new units (cells) formed by division of the cells of the growing point (p. 7) To demonstrate this fact we take a number of seedlings having straight radicles which should be about an inch long and, using Indian ink, mark off horizontal lines (see Appendix II) along the root, at intervals of one millimetre from the apex backwards (Fig. 16 A). The seedlings are then attached to a piece of cork by pins passing through the cotyledons and fixed with the roots pointing vertically downwards in the neck of a jam-jar, the sides of which are lined with wet blotting-paper. The whole should then be put in a warm dark place for about forty-eight hours. If the roots be now examined, it will be found that the marks are no longer at equal intervals, but that some have separated more or less appreciably, whilst others have practically remained at the original distance of one millimetre (Fig. 16 B). Little elongation has taken place, for example, between the lines at the extreme tip, or between those on the part of the root adjacent to the seed. On the other hand, the distance between the fourth and fifth marks has increased very considerably, while the intervals above

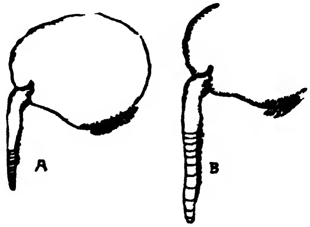

FIG. 16.—Experiment to demonstrate region of growth in radicle of Broad Bean (about half the natural size). A, At the beginning of the experiment. B, Forty-eight hours later.

and below will be found to have elongated to a less and less extent until we reach the regions at base and apex where, as we have seen, no alteration has taken place.

It is thus apparent that growth in length of the root takes place in a very restricted zone, situated a little way behind the apex. It will also be gathered that growth involves two distinct processes, viz. the actual division of the cells of the growing point resulting in the formation of new units, and the subsequent enlargement of these, mainly in the longitudinal direction, until they have reached their adult dimensions.

It is obvious that, in order to pierce its way through the soil, the growing root must be capable of exerting considerable force. This is a result of the increase in size of the cells in the zone of elongation and in nature, where the older part of the root is firmly fixed by root-hairs and lateral roots, it serves to drive the apex downwards. Moreover, owing to the restriction of growth in length to a short region, the driving power is exerted close to the apex, and therefore the direction of application of the force and the moving tip tend to remain in the same straight line; thus a maximum effect is secured. The growing part of the root is comparable to a short nail driven into a piece of wood. On the other hand, a long slender nail, in which the driving force is applied some distance from the point, is very liable to become bent, and the same statement would apply to a root in which the zone of elongation was situated some way from the tip.

We have already noticed that the root-hairs arise above the elongating portion of the root, and the advantage of this is clear when we remember that their purpose is to absorb water from the soil (p. 8), a function which could not be fulfilled if their position were continually altering with the growth of the root. Moreover, under such conditions the delicate root-hairs would become torn and useless. As it is, however, they always develop from that part of the root which has just concluded its growth in length. The root-hairs, which are narrow tube-like outgrowths of the surface-cells (Fig 74, p. 154), insinuate themselves between the small particles of the soil (Fig. 17, *r.h.*), with many of which they come into very close contact. It is owing to this that even after careful washing small soil-particles still cling to the finer branches.

The soil, considered physically, is an aggregation of two kinds of particles. On the one hand we have the mineral particles formed by the breaking down of rocks under the influence of atmospheric and other agencies; on the other hand we have the organic particles (*humus*) consisting of the decaying remains of plants and animals that have previously lived on the soil in question. But, in addition to the dead matrix, the soil contains a teeming population of microscopic animal and vegetable organisms, some of which are essential to the well-being of the larger plants.

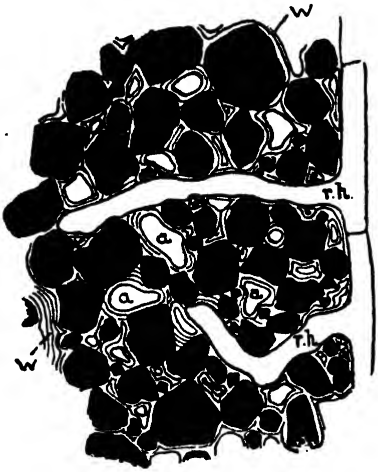

Fig. 17.—Diagram of soil with root-hairs (*r.h.*) to show the distribution of air (*a*) and water (*w*) (much enlarged). Soil-particles in black.

Different soils influence vegetation by the amount and kind of mineral substances they contain and their capacity for holding water. This latter depends on the degree of fineness of the component particles, since the soil-water mainly occurs as films around them (Fig. 17), the larger spaces being occupied by air. The contrast between a dry sandy soil and a damp clay containing a large proportion of particles less than ·002 mm. in diameter is in this respect very striking. The humus being colloidal in nature (cf. p. 70) also presents a large water-retaining surface. The thin films surrounding the soil-particles comprise the soil-solution, which is absorbed by the root-hairs.

It is not only the front part of the root that is devoid of root-hairs, for it is seen that the latter usually occupy a short zone and that the hinder part is again bare (Fig. 15). This is because root-hairs are mostly transient structures lasting only a few days, new hairs sprouting out in front as the older ones die away behind. The new hairs arise from surface-cells in which elongation has just ceased and thus, whilst the part occupied by root-hairs always remains at the same distance from the root-apex, the hairs follow the growing tip as it penetrates through the soil. Since root-hairs are developed in exactly the same way on the lateral roots, the growth of the whole root-system carries the region of absorption into new areas of the soil.

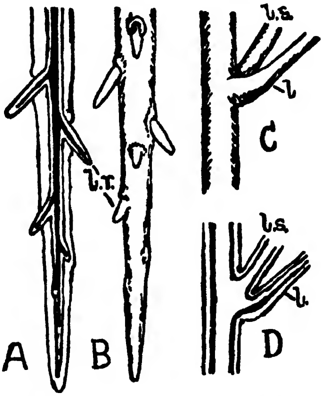

FIG. 18.—Diagram to explain the origin of lateral roots and shoots. A, Longitudinal section of root. B, Exterior view of same. *l.r.*, lateral root. C, Exterior of node of stem. D, Longitudinal section of same. *l*, leaf; *l.s.*, lateral shoot.

The side-roots will be found to arise at some considerable distance from the tip of the main root (Fig. 9 C, Fig. 11 E), and careful observation shows that they have burst through the outer covering of the latter (Fig. 18 B). If we now cut the main root lengthwise into two equal halves with a sharp pocket-knife, it will be seen (Fig. 18 A) that the branch-roots arise from the central core of hard substance with which we have already become familiar in the Shepherd's-purse (p. 2) and which is a feature of all roots. A short distance behind the apex young laterals, which have not yet reached the surface, are distinguishable (Fig. 18 A), whilst farther back others are seen piercing through to the exterior. The laterals thus originate in the interior of the parent-root, and the branching of the root is therefore described as *endogenous*. In this way the young branch is nurtured within the mother-root, until it has developed a root-cap and can make its own way through the soil. It would moreover clearly be unsuitable for the laterals to emerge from the portion of the root undergoing elongation or bearing root-hairs. It will be noticed that the side-roots do not arise indiscriminately from the main root, but that they form a number of vertical rows, generally four or five (Fig. 18 B, Fig. 12 A, p. 30).

We have thus come to recognise the following regions in the main root: the root-cap, the growing point, the zone of elongation, the zone of root-hairs and the mature zone bearing laterals. All, even the finest members of the root-system, show an identical structure, and the principal difference between the main root and its branches lies in their direction of growth. We have frequently had occasion to remark that the main root grows vertically downwards into the ground, and we will now enquire as to the reason. To solve this problem the following experiment may be performed.

A number of healthy seedlings which should have straight radicles are pinned parallel to one another to the surface of a large cork; the latter is then fixed edge on by means of a nail to the bottom of a large light-tight box in such a way that the radicles are horizontal and free to bend. The entire inner surface of the box (including the lid) is lined with wet blotting-paper, and the whole is then left in a warm place for about twenty-four hours. If the radicles are then examined, the tips will be found to have curved downwards into a vertical position. It is plain that the roots were subjected equally on all sides to moisture, warmth, supply of air and darkness, and the only one-sided influence lay in the force of gravity acting towards the centre of the earth. The root then, unlike the shoot of most plants (cf. p. 19), grows in the direction of this force and is thus led to penetrate deeper and deeper into the soil. On the other hand, light which, as we have seen, plays an important part in determining the direction of growth of the shoot, has little influence on the roots of most plants.

Examination of the root-system of such plants as the Shepherd's-purse and the Pea at once discloses the fact that the laterals diverge at more or less of an acute angle from the main root, so that they grow outwards and downwards (Figs. 2, 9, 11), a direction likewise influenced by gravity. Arising from these laterals of the first order are smaller roots of the second order, and in a strongly developed root-system there may even be branches of a higher order (Fig. 2). These ultimate members of the root are unaffected by gravity and generally extend into the soil in all directions. Hence the volume of soil occupied by the root-system is very completely exploited by its numerous ramifications.

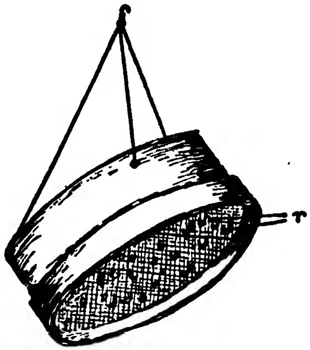

Fig. 19.—Experiment to demonstrate hydrotropism in roots. For description, see text. *r*, the curved radicles.

Apart from gravity, there is, however, one other condition that markedly influences the direction of growth, especially of the finer branches of the root-system, and that is the distribution of moisture, whose influence is described as ***hydrotropism***. To demonstrate this fact a small wire sieve is filled to the depth of about half an inch with damp sawdust in which Cress-seeds are sown, the whole being then covered with blotting-paper which is kept wet. After this the sieve is suspended in moderately moist air at an angle of about 45°, whilst a second similar apparatus is hung up horizontally. When the radicles of the Cress-seedlings emerge through the meshes of the sieve they will be found in the case of the sloping one to curve through a right angle, so that they again reach the damp sawdust (Fig. 19 *r*). This is due to the vertically growing radicles, on entering the relatively dry air below the sieve, being nearer to the moist surface on one side than on the other, and hence the necessary conditions for a hydrotropic curvature are realised. On the other hand, in the horizontal sieve, no such curvature is observed, since all sides of the radicles are equally stimulated by the moisture.

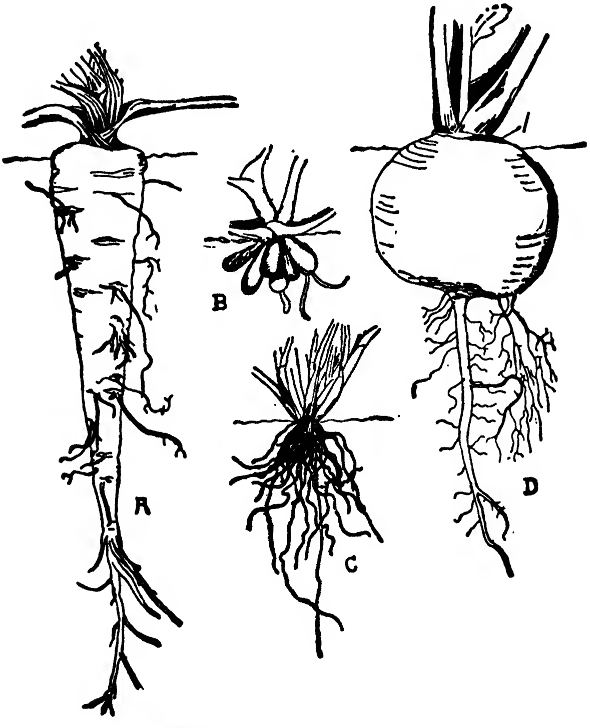

FIG. 20.—Different types of root-systems (reduced to about half natural size). A, Carrot. B, Lesser Celandine. C, Grass. D, Turnip. The level of the ground is in all cases shown by a black line. *l*, leaf-scar.

The type of root-system with which we have hitherto become familiar (*e.g.* in the Shepherd's-purse, Fig. 2; the Pea, Bean, etc., Fig. 9) is characterised by the possession of a prominent main root (often spoken of as a *tap-root*) growing vertically down into the soil and bearing numerous branches that become progressively smaller. This type is most commonly found in Dicotyledons. In Monocotyledons, on the other hand, as well as in many Dicotyledons, the root-system consists of a number of members in which we cannot distinguish any single one as specially prominent; such a root-system is described as *fibrous*, and good examples are furnished by the Hyacinth and Grasses (Fig. 20 C).

The root-systems of large trees consist of two parts, the large woody anchoring roots and the fine thread-like branches which serve for absorption of water; these latter are usually located beneath the drip of the tree.

In many biennials and perennials the roots serve as storage organs for food-materials laid up for subsequent growth (see Chapter II), and in consequence are more or less swollen (Fig. 20). Such cases include a number of our common vegetables, which owe their utility to the large quantities of food-substances present (*e.g.* Carrot, Beetroot, Parsnip, etc.).

CHAPTER V

THE SHOOT

THE shoot, as we have already learnt, in the majority of cases grows erect in obedience to the directive influences of light and gravity (p. 19), though occasionally it may exhibit a prostrate or climbing habit (see p. 20). Quite apart, however, from these broad distinctions, the shoot differs greatly in appearance from plant to plant, so that we are generally not at a loss to know one kind from another. This variety of form is determined by the way in which the stem branches, by the mode of arrangement of the leaves and by their shape, and we shall therefore not be in a proper position to understand the architecture of the shoot until we have considered all these points separately.

It is easiest to study the phenomena of branching first on woody plants, because the succession of events is more clearly seen in them than in herbs which frequently do not branch much until the time of flowering. If we examine a woody shoot, as for instance one of the larger branches of the Beech, in winter-time (Fig. 21), we find that it is terminated by a long, slender and pointed structure of a brown colour, the *terminal bud* (*t.b.*); this contains in miniature and telescoped together next year's continuation of the branch. Along the sides of the latter are a number of perfectly similar buds (the *lateral buds*, *l.b.*), each capable in the next season of growing out into a side-branch. Beneath each lateral bud the bark shows a somewhat kidney-shaped smooth scar (*l.s.*), generally well defined and bearing a curved band of dots. Each scar marks the former point of attachment of a leaf (*i.e.* it is a *leaf-scar*, see also Fig. 22), and the dots on its surface are the broken ends of the strands joining stem and leaf (p. 8). It will be seen, therefore, that the lateral buds are all axillary (p. 2) to leaves of past seasons, the terminal buds alone having no subtending leaf-scars.

The colour and shape of buds and leaf-scars and the mode of arrangement of the strands on the latter varies so much in different trees and shrubs that it is not difficult to recognise them in winter by such characters. Other external features are provided by the *lenticels* (Fig. 21, *l*; Fig. 22), small generally lighter-coloured projections of varying shape, which are irregularly distributed on the bark of woody plants and serve the purpose of gaseous interchange between the interior of the branch and the atmosphere (cf. p. 151), prevented except at these points by the impermeable bark.

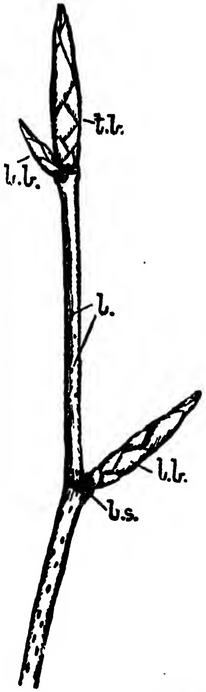

Fig. 21.—Portion of a twig of the Beech in winter-time (about natural size). *l.*, lenticels; *l.b.*, lateral buds; *l.s.*, leaf-scar; *t.b.*, terminal bud.

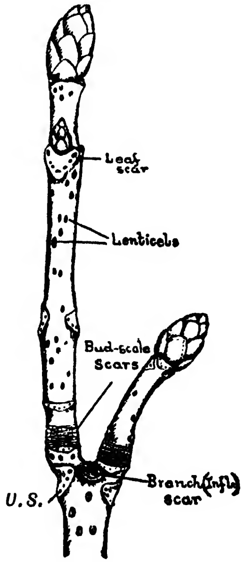

Fig. 22.—Portion of twig of Horse Chestnut showing buds, leaf-scars, and lenticels (about two-thirds natural size). *v.s.*, vascular strands.

In such early-flowering plants as the Horse Chestnut and Ash, the inflorescences in miniature are already contained within the winter buds, in which they occupy the termination of the axis. When flowering and fruiting are over and the stalk of the inflorescence dies away, it leaves a large round somewhat sunken scar (Fig. 22, infl. scar), whilst the nearest lateral bud shifts into the line of continuity and in the next season replaces the branch whose further growth terminated with the production of flowers. Scars marking the former points of attachment of inflorescences are always to be found on branches of the Horse Chestnut and Ash, and must be distinguished from the horseshoe-shaped leaf-scars.

The extent to which branching is carried on varies greatly; on the one hand we have plants, like most Monocotyledons, in which it is practically restricted to the region of the inflorescence, whilst on the other we have richly branching trees, such as the Beech or Elm. In all woody plants, however, the materials available for growth suffice for the development of only a small number of the buds, a very considerable percentage being doomed to inactivity, either permanent or temporary. These inactive or *dormant buds* retain their vitality often throughout the life of the tree or shrub, and are ready to grow out into branches, should occasion demand. That it is lack of nourishment which in many cases prevents them from developing further is easily seen if we remove the terminal portion of any given branch; thereby lateral buds borne lower down upon it which would otherwise remain dormant are caused to sprout. Upon this depends the principle of hedge-making, in which by cutting off the tops of the upper branches numerous laterals are caused to develop, so that a dense growth results.

In the case of the root we found that the laterals arose endogenously (p. 40, Fig. 18 A and B), but the branches of the stem, as also the leaves, are readily seen to originate from the surface-tissues only (cf. Fig. 18 C and D, Fig. 28), *i.e.* they are *exogenous.* The protection afforded to the young lateral root as a result of its internal origin is unnecessary in the case of the branches of the stem, where no such resistance, as the soil offers to the growth of the root, has to be encountered. It should also be noted that the region of elongation of the shoot is much longer than in a root (cf. p. 37).

The majority of plants exhibit but a single leaf at each node, an arrangement which is described as *alternate*; but there are quite a large number of plants (*e.g.* Horse Chestnut, Fig. 22; Chickweed) in which a pair of leaves arise together, when the leaf-arrangement is said to be *opposite*. Such pairs of leaves almost invariably occur at right angles to one another at successive nodes, so that the leaves do not overshadow one another.

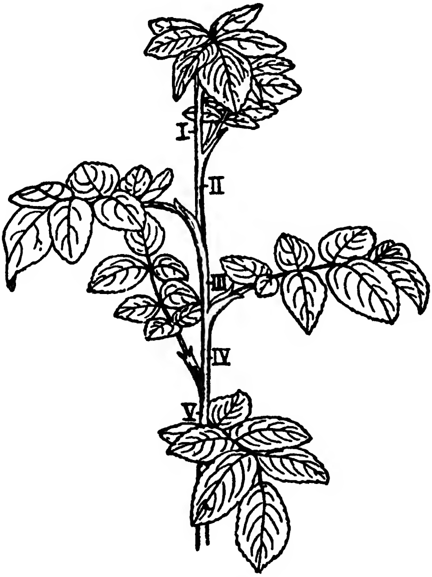

FIG. 23.—Portion of a twig of the Rose, showing the way in which the alternate leaves are arranged. The successive internodes are numbered I–V.

In other cases (*e.g.* some water-plants) more than two leaves occur at a node, such a group being spoken of as a *whorl*.

It is important to realise that leaves are not scattered irregularly over the shoot, but are disposed according to some definite, even though slightly variable, plan. By far the commonest is a spiral arrangement (Fig. 23), and, if we make a projection of such a leaf-arrangement (*i.e.* a plan as though viewed from above), we shall find that the arcs between successive leaves are approximately equal. As a consequence superposed leaves (*i.e.* in the same vertical line) are usually separated by two or more internodes, so that the shading effect of one leaf by another is minimised.

It is, however, only in erect shoots that the leaves retain throughout life the positions which they occupied at their first development. In the case of the horizontal branches of trees and shrubs the matter is different; the leaves show the same original arrangement as on the upright branches, but during development the position of the blades is altered and replaced by an arrangement more suited to the direction of illumination. This is very clearly seen, if one compares an upright and horizontal branch of a Privet or other plant with opposite leaves. On the erect branch the original arrangement is quite distinct, but on the horizontal one the leaf-stalks have twisted so that the blades are placed more or less horizontally at right angles to the light, the former position of the leaves

FIG. 24.—Photographs of two branches of the Hornbeam; on the left a horizontal branch showing leaf-mosaic, on the right an upright shoot showing radial arrangement of the leaves. [Photo E. J. S.]

being only made out by a careful scrutiny of their mode of attachment.

The same feature can be observed in the Beech and Hornbeam (Fig. 24), where on the side-branches the leaves all appear in one plane instead of being radially disposed in a number of vertical series. Whilst leaves are able to adjust their position in this way before they attain to maturity, this is not usually possible after the leaf is fully grown (see, however, p. 213); a position is therefore taken up during development, such as is best suited to light-reception.

FIG. 25.—Photograph of seedling Sycamore taken from above to show leaf-mosaic. [Photo E. J. S.]

The preceding considerations indicate that we must distinguish between shoots in which the leaves and branches spread out in all directions from the central axis (*radial* shoots, *e.g.* in most erect plants), and those in which the leaves and branches lie in one plane (*dorsiventral* shoots, *e.g.* horizontal and creeping stems). For, in the latter case, the axillary buds tend to grow out in the plane of the leaves, as is well seen in the horizontal branch-systems of Hornbeam (Fig. 24), Elm or Beech. In fact, there is here one almost continuous expanse of leaf-surface, smaller leaves being situated between the larger ones and those of neighbouring branches overlapping only to a very slight extent, so that we can speak of a *leaf-mosaic*, a feature which is always pronounced in trees with a dense canopy and in smaller plants growing in the shade of larger ones. Such leaf-mosaics are also exhibited by radial shoots (*e.g.* in seedlings of the Sycamore, Fig. 25).

The foliage-leaf as a general rule consists of three parts (Fig. 27):

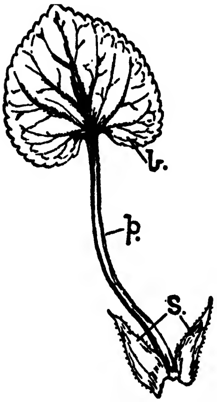

FIG. 26.—Leaf of the Sweet Violet (about three-quarters the natural size). *b.*, blade; *p.*, petiole; *s.*, stipules.

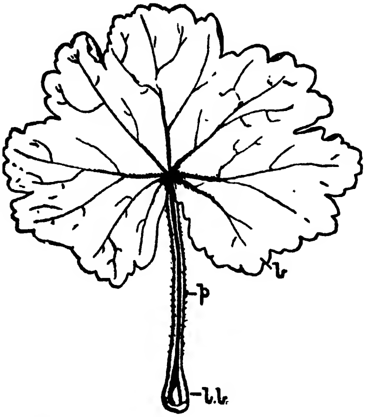

FIG. 27.—Leaf of the Garden Geranium (about half the natural size). *b.*, blade; *l.b.*, leaf-base; *p.*, petiole.

the base or slightly enlarged attachment to the stem (*l.b.*), the stalk or petiole (*p.*) whose upper surface is generally grooved or flat, and the blade or lamina (*l.*). Sometimes the leaf-base assumes considerable proportions and forms a large sheathing structure, as in many members of the Carrot-family (Umbelliferæ); whilst in other cases, though the leaf-base itself is small, it develops lateral outgrowths which are termed *stipules* (Figs. 23, 26, *s*). Both the enlarged leaf-base and the stipules probably serve in the majority of plants for the protection of the young axillary bud.

Occasionally the petiole is absent, as, for example, in the upper *sessile* leaves of the Shepherd's-purse (p. 5, Fig. 1), but the majority of leaves are *petiolate.* The petiole plays an important part, not only as an organ for spreading out the blade to the light and air, but also, as we have just seen, by placing the latter in the most suitable light-position; it also serves as a means of communication between stem and leaf-blade, and through the hard vascular strands which traverse its length and join up on the one hand with the veins and on the other with similar strands in the stem (p. 8), food-substances travel to and from the leaf.

The leaf-blade may consist of one continuous undivided surface, in which case it is described as *simple* (Figs. 26, 27); or it may be cut up into a number of lobes connected with one another by an undivided portion, when the leaf is said to be *lobed* (Fig. 25); or again it may be completely segmented into a number of separate leaflets, when it is known as *compound* (Fig. 23). Compound leaves are readily distinguished from branches bearing small leaves by the presence of a bud in the axil of the main stalk, by the absence of axillary buds to the individual leaflets, and by the absence of a terminal bud.

Such leaf-features are often very characteristic of whole groups, and thus furnish aids to the identification of plants in the vegetative state. For example, in most Monocotyledons the leaves have a narrow elongated blade and are devoid of a stalk; in the members of the Carrot-family (Umbelliferæ) they are generally much divided and without stipules, whilst stipulate compound leaves characterise most members of the Pea-family (Leguminosæ). On the other hand, simple undivided leaves are a feature of the Pink-family (Caryophyllaceæ). The comparative uniformity, with respect to leaf-form and arrangement, amongst members of the same family, despite the diverse habitats in which they grow, indicates that heredity rather than environment is the chief cause of variation in leaf-form.

From a consideration of the mature shoot we can now pass to a study of its early development, material for which is furnished by every bud. The essential structure is always the same, and may for the sake of convenience be examined in a Brussels Sprout,[1] a bud in which, owing to its large size, all the parts are easily recognised. Outwardly we see merely a series of overlapping leaves, but a more complicated structure is presented when the bud is halved lengthwise (Fig. 28). The central

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[1] The Cabbage is likewise a huge bud, each Brussels Sprout being a Cabbage on a small scale.

portion is occupied by the stem which tapers to the growing point (*g.pt.*) above. On either side of the latter is seen a series of developing leaves (*p′*, *p″*, *p‴*, etc.), the youngest and

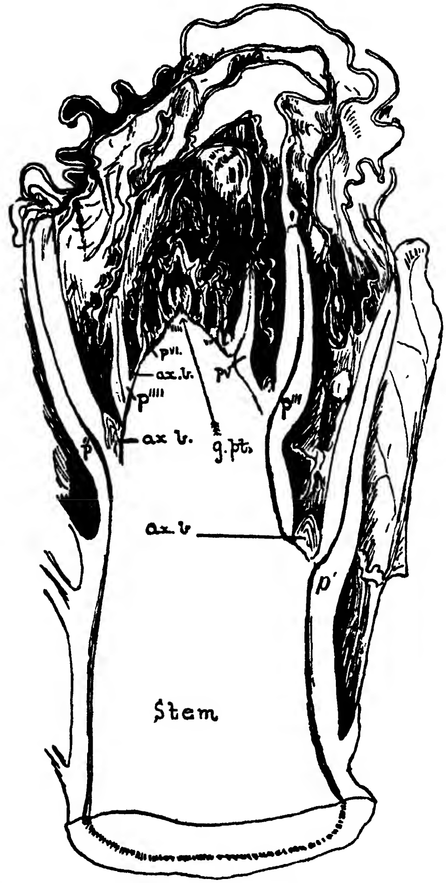

FIG. 28.—Section of Brussels Sprout (considerably enlarged). *ax.b.*, axillary buds; *g.pt.*, growing point of main axis; *p′*, *p″*, *p‴*, etc., leaves of successive ages.

smallest nearest the growing point, the oldest and most advanced farthest from it. A very short distance behind the growing point minute buds (*ax.b.*) are seen arising in the axils of the young leaves and, as we get farther away from the apex, the former become more and more prominent until each is recognised as having the structure of the main bud in miniature. It will be noticed that the young leaves are closely crowded together and that the upper internodes are scarcely developed; consequently there is insufficient room for the enlarging leaf-blades which become thrown into numerous folds, and thus we obtain the familiar compact structure of a bud.

The Brussels Sprout is an example of a summer-bud in which the close packing gives sufficient protection to the young structures developing within, although even here the whole is enveloped in maturer leaves. In buds which have to withstand the rigour of winter additional protection is, however, necessary and this is provided in a number of different ways. Most commonly the bud is covered in by close-fitting leathery or membranous scales (the *bud-scales*), which are frequently brown (*e.g.* in Beech, Oak, Horse Chestnut), but sometimes black (*e.g.* in the Ash), and usually exhibit the same arrangement as the leaves upon the stem (*e.g.* the opposite scales of the Horse Chestnut, Fig. 22, and the alternate ones of the Lime and Elm).

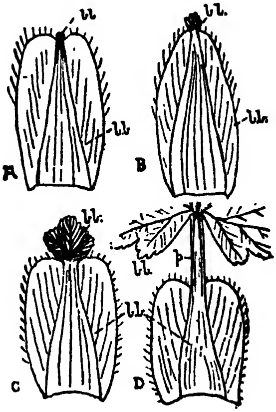

FIG. 29.—Transition between bud-scales and foliage-leaves in Flowering Currant; the successive stages are marked A–D and are all about twice natural size. *bl.*, blade; *l.b.*, leaf-base; *p*, petiole.

At first sight a bud-scale appears to differ very much from a foliage-leaf, but an examination of the opening buds of the Flowering Currant, for instance, will show that the one is but a modification of the other. If, starting at the outside, the bud-scales are removed in succession, a gradual transition will be found between them and the foliage-leaves within the bud (Fig. 29). The outermost scales are oval with a minute black apex (Fig. 29 A, *bl.*) ; a little further in, the scales show a somewhat larger tip, which on careful scrutiny is seen to be a rudimentary or arrested leaf-blade (Fig. 29 B, *bl.*) ; still further in, the latter becomes more prominent (Fig. 29 C), and so by successive stages we come to the first foliage-leaves in which a petiole (Fig. 29 D, *p*) appears and in which the scaly enlargement at the base (*l.b.*) shows a diminution in size. In the innermost leaves of the bud this scale is seen to have contracted into a small leaf-base, such as we find in the mature foliage-leaves of the plant.

The transition just described shows plainly that the bud-scales of the Flowering Currant are nothing else than leaves with a much enlarged leaf-base and a more or less completely arrested lamina. The same sequence can be observed in the bud-scales of many other plants, such as the Sycamore, Ash, Horse Chestnut, etc., although it is not always the leaf-base that forms the bud-scale. Thus, in the Lilac and Privet the bud-scales are formed from entire leaves.

Bud-scales are not always the only special protection of the winter-bud, for not uncommonly there is a layer of sticky varnish (*e.g.* Horse Chestnut, Poplar), which not only glues the scales together, but further reduces the risk of excessive transpiration (cf. pp. 9 and 18) from the young leaves within. Moreover, the latter are often equipped with numerous hairs, appearing as a white wool in the Horse Chestnut or as a dense brown covering in the Plane Tree, and, as we shall learn later (p. 133), such hairs constitute a very efficient protection to the leaves.

With the arrival of spring all the different parts within the bud begin to expand, the hitherto short internodes commence to lengthen out and the leaves to unfold, this taking place at the expense of the food-materials which, as described on p. 18, are stored up in the woody branches. As a result the whole bud swells, the bud-scales are forced apart, and the shoot begins to elongate. Usually no lengthening of the internodes takes place between the bud-scales, which consequently remain as a crowded group at the base of the growing shoot. Sooner or later they drop off, leaving a number of broad flat scars which, on superficial observation, look like a series of closely set rings encircling the stem (see Fig. 22); since such *bud-scale scars* are necessarily formed only at the beginning of each season, the intervals between successive series mark as many years' growth of the branch.

CHAPTER VI

THE STRUCTURE AND PHYSIOLOGY OF THE PLANT-CELL

EVERY living organism, whether animal or plant, is composed of one or more minute units called *cells*, and this applies even to those forms of life which are so small that they can only be seen with the help of a microscope. The green powdery covering so often present on tree-trunks and palings consists of multitudes of single-celled plants (*Pleurococcus*, Fig. 103, p. 224), whilst millions of cells together form the body of a garden weed or tree. Organisms of the latter type are described as ***multicellular***, whilst those consisting of a single cell are termed ***unicellular***. The structure of the living cell is fundamentally the same both in plants and animals.

The size of a cell varies greatly. In certain of the unicellular Bacteria it is less than 0·001 mm. in diameter, whilst in some fleshy fruits the cells are 1 mm. wide; in special cases (*e.g.* fibres of the Hemp) they may even be as long as 10 mm. The strictly multicellular plant consists of units whose living contents are joined together (p. 78), whilst in many colonies the union of the cells is a mere mechanical adhesion. In the former case there is usually a marked interdependence of the constituent units which exhibit differentiation among one another and division of labour.

The structure of a cell will best be realised if a typical example is studied, such as that obtained by stripping off the skin (or *epidermis*) from the inner surface of an Onion-scale. If a small portion of this be mounted in water, and examined under the low power of a microscope (see Appendix IV), it will be seen to consist of a large number of oblong cells connected together without any intervening spaces to form a ***tissue*** (Fig. 30, A). The network of delicate lines separating the individual units is constituted by the *cell-walls*, which are all joined to one another. In each cell a colourless, somewhat dense granular substance (the *cytoplasm*, Fig. 30, B, *Cy*.) is visible, particularly around the edge, whilst near the centre or against one side is situated a rounded shining body, the *nucleus* (Fig. 30, B, *N*).

These cells consist, then, of three parts, the cell-wall (Fig. 30, B, *C.W.*), which is not living and is merely a protective case, the cytoplasm, and the nucleus; the last two constitute the living part or *protoplast*, composed of protoplasm. The latter is probably a very complex mixture of proteins (cf. p. 101), fatty bodies, etc., composed mainly of the elements carbon, hydrogen, oxygen, nitrogen, and sulphur (often together with phosphorus, especially in the nucleus). It has somewhat the consistency

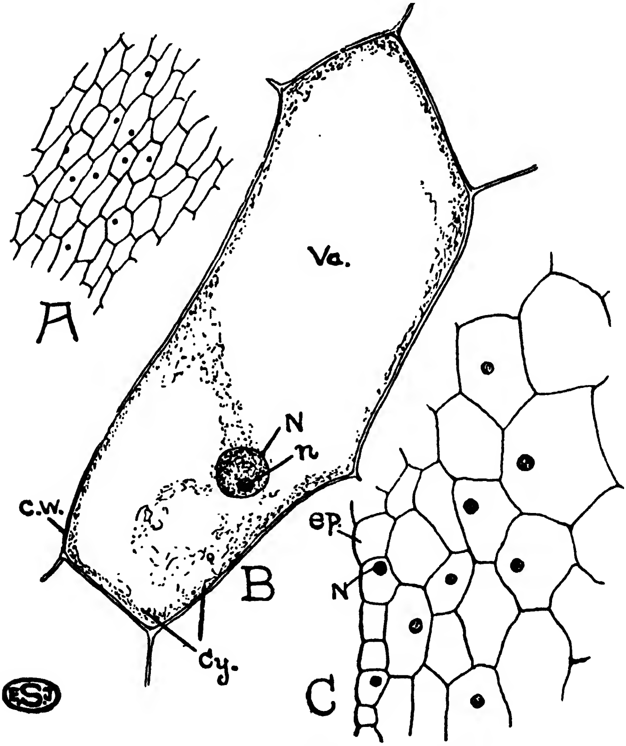

Fig. 30.—Epidermis of Onion bulb-scale. A, small portion in surface view. B, a single cell much enlarged. C, a scale in vertical section. In A and C the nuclei are shown black. *Cy.*, cytoplasm; *C.W.*, cell-wall; *ep.*, epidermis; *N*, nucleus; *n*, nucleolus; *Va.*, vacuole.

of the white of an unboiled egg, and usually contains large numbers of small granules which are partly of the nature of food-bodies and partly waste-products. The fact that not all, though some, of the properties of living protoplasm are exhibited by cells which are ground to pulp suggests that the particular characteristics of the cytoplasm are not entirely an outcome of its chemical constitution, but are to some extent a consequence of its ultimate structure. The nucleus is the most important part of the protoplast, a fact which will become more apparent in later chapters (p. 332), when the reproductive processes of plants are studied. It appears to be essential for many of the vital activities of the cell. A demonstration of this is afforded by the fact that, if the unicellular animal *Stentor* is broken into pieces, the fragments which contain portions of the nucleus develop into new individuals, whilst the others, after a short time, perish. Moreover, the nucleus is generally found in that part of the cell which is in process of active growth, *e.g.* at the tip of a growing root-hair (cf. Fig. 74).

The structure of the Onion-cell can be more clearly distinguished if the strip of epidermis be stained with a drop of iodine (see Appendix I), and a single cell examined under the high-power objective. The protoplasm will have assumed a yellowish tint, whilst the nucleus appears pale brown. This colour reaction of the protoplast is one characteristic of proteins generally. The nucleus (Fig. 30, B, *N*) is bounded by a thin ***nuclear membrane***, whilst within it one or two small round bodies, the ***nucleoli*** (*n*), are now plainly visible, since they are stained more deeply than the rest. The cytoplasm does not completely fill the cell, but there is a large space or *vacuole* (*Va.*) occupying the greater part of the central region; this vacuole, apparently empty, is in reality filled with a watery fluid, the *cell-sap*. Close observation shows that the cytoplasm is not evenly granular throughout, but that there is a very thin clear layer immediately within the cell-wall. This layer is a result of physical forces operating at the surface of the cytoplasm, and a similar clear layer can be detected at the surface abutting on the vacuole. These layers are spoken of as the ***plasmatic membranes***.

If another strip of Onion epidermis be mounted in concentrated sulphuric acid, the cell-walls will swell and disappear.

Subsequent addition of iodine gives a blue colouration to the dissolving walls, a reaction characteristic of *cellulose*, of which most thin cell-membranes largely consist.

It must be realised that the cells just examined, like all plant-cells, are developed in three dimensions, a fact which can be verified by cutting a section transversely across the Onion-scale, when the epidermal cells will appear as flat tabular structures (Fig. 30, C).

As a second example, one of the cells forming the purple hairs (Fig. 31, A) on the stamens of the Common Spiderwort (*Tradescantia*) may be examined.[1] These show the same structure as those of the Onion, but the cell-sap is here of a purple colour. The nucleus, surrounded by a small mass of cytoplasm, is not uncommonly suspended in the middle of the vacuole, the enveloping cytoplasm being connected with that lining the cell-wall by a number of protoplasmic strands (Fig. 31, B). If the granules in these strands are closely observed, they will be seen to exhibit a continuous streaming movement which can be accelerated by *slight* warming, but ceases on the addition of a poison (*e.g.* alcohol), whereby the cell is killed. A temporary cessation of the movement can be brought about by mounting the cells in water to which a trace of some anæsthetic (*e.g.* chloroform) has been added. On returning the hairs to ordinary water, however, streaming of the granules is soon resumed. A similar effect is obtained if the cells are mounted in water which has been boiled and subsequently cooled, the result showing the necessity of oxygen for the performance of such movements. The movement is really due to a flowing of the cytoplasm, and this phenomenon betrays the fluid consistency of the latter. No movement can be recognised, however, in the plasmatic membranes, which are therefore probably of a denser character.

All living plant-cells display the features above described, but in many cases other structures are present, and of these the commonest are bodies known as *plastids*. In those cells of the plant which are exposed to the light the plastids become the depositories of the green pigment, or *chlorophyll*, and are then

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[1] If material of the Spiderwort is not available, a good substitute is furnished by the unicellular hairs lining the inner surface of the corolla-tube of the White Dead-nettle, in which, however, the cell-sap is uncoloured.

known as *chloroplasts*. On examining a leaf of the Canadian Pondweed (*Elodea canadensis*) under the high power, each of the more or less rectangular cells will be found to contain a number of chloroplasts, which will be seen from one of two aspects (Fig. 32). Some, situated along the sides of the cell, are viewed in profile and appear as flattened ellipses (*O.S.*), whilst others lying against the upper or lower walls, and consequently seen from the surface, present a round or oval form (*Su.*). Each chloroplast is thus a solid body which has more or less the shape of a biconvex lens.

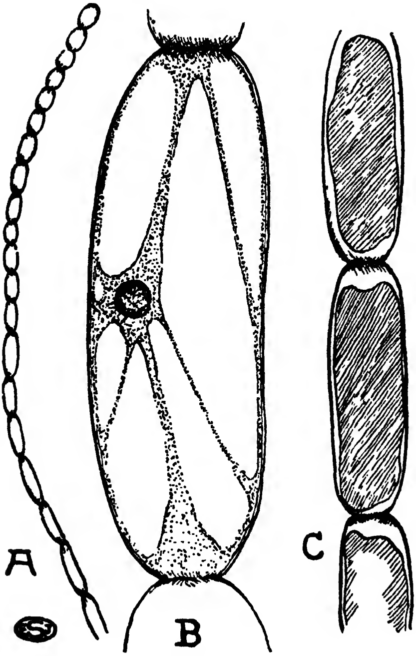

FIG. 31.—Staminal hairs of the Spiderwort (*Tradescantia*). A, a single hair; B, a single cell showing the nucleus and strands of cytoplasm passing across the vacuole; C, a hair plasmolysed with sea-water.

If attention be centred on a single cell, the chloroplasts lying against the upper face can be brought clearly into view by turning the fine adjustment; on focussing to a lower level, however, another layer of chloroplasts appears belonging to the same cell. We can thus liken each cell to an oblong box lined along the whole of the inner surface with a thick viscid fluid (the cytoplasm) in which are embedded the chloroplasts, the cavity of the box representing the vacuole (Fig. 32, *Va.*) with its cell-sap.

By watching the chloroplasts, particularly in the elongated cells of the midrib, they will be observed to exhibit movement similar to that of the granules in the cells of the Spiderwort, and here as there this is actually due to a flow of the cytoplasm.

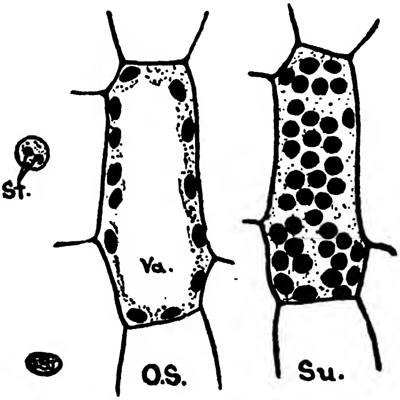

FIG. 32.—Two cells of the Canadian Pondweed, one in surface view (*Su.*), and the other in optical section (*O.S.*). The chloroplasts are shown black. At the left a single chloroplast showing starch grains (*St.*). *Va.*, vacuole.

Such a streaming movement probably takes place in the cytoplasm of all living cells, but in many cases it is so slow that it cannot be demonstrated. By its means food-substances, etc., are more quickly distributed from one part of the cell to the other than by mere diffusion.

When leaves of the Canadian Pondweed, or those of other plants, are kept in spirit for some little time, all the chlorophyll is removed in solution. The chloroplasts, though now colourless, have undergone no change of shape, and are therefore merely specialised parts of the cytoplasm which held the chlorophyll.

The green cells of all the higher plants contain numerous chloroplasts, essentially similar in form to those just studied. In the simple types of plant-life (*e.g.* among the Algæ), however, the cells are often provided with but a single chloroplast or a limited number of them, and these are frequently of a much more elaborate pattern. *Spirogyra*, which is exceedingly common in stagnant water, furnishes an extreme instance. The plant here consists of a single thread or filament composed of cylindrical cells joined end to end. According to the species, each cell contains, apart from the cytoplasm and nucleus, one or more chloroplasts in the shape of green spiral bands, usually with a jagged edge (Fig. 33, *ch.*). These spiral chloroplasts are here, again, situated in the lining layer of cytoplasm. At intervals bright bodies, consisting of protein and known as *pyrenoids*, are

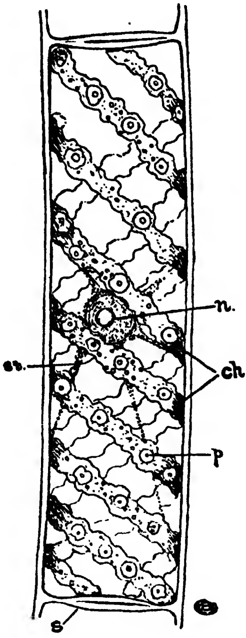

FIG. 33.—Single cell of a *Spirogyra* filament showing the spiral chloroplast (*ch.*), the pyrenoids (*p.*) surrounded by starch, and the nucleus (*n.*) supported by cytoplasmic strands (*st.*). *S*, separating wall between adjacent cells.

embedded within their substance (Fig. 33, *p.*); but these are more evident after treatment with iodine, whereupon they become blue, owing to the fact that each is surrounded by a layer of starch. Pyrenoids are not found in the chloroplasts of the higher plants, but are quite frequent amongst the Algæ (see p. 218).

Returning to the cells in the hairs of the Spiderwort, we will mount them in 2 per cent. natural or artificial sea-water (see Appendix III); the resulting phenomena could be equally well observed by using any cells with coloured sap, *e.g.* those forming the lower epidermis of the Mother-of-Thousands (*Saxifraga sarmentosa*), or those in the petal of a Pæony. In the cells thus treated the lining layer of cytoplasm has contracted away from the wall, so that a clear space is visible between it and the latter (Fig. 13, C). In this condition the cell is said to be *plasmolysed*, and the phenomenon is spoken of as *plasmolysis*. If the sea-water be replaced by tap-water, the cell-sap increases in volume, so that the plasmatic membrane regains its original position pressed up against the wall, and the cell resumes its normal appearance. By alternately substituting sea-water and tap-water, this sequence of events may be repeatedly observed.

In the normal cell the pressure of the sap within the vacuole keeps the lining layer of cytoplasm distended and forced against the wall, in much the same way as the bladder of a football, when inflated with air, is pressed against the leather cover. If the air be allowed to escape, the bladder shrinks and a space is left between it and the cover. Similarly, the contraction of the protoplast of the cell, when surrounded by sea-water, must be attributed to a decrease in volume of the cell-sap owing to passage of water into the outside liquid. The recovery, when placed in water, obviously implies an increase in volume of the sap, and this can only be due to some of the water around having passed into it.

It is a well-known physical phenomenon (*osmosis*) that, when two solutions of different concentrations are separated by a membrane (which may be of a fluid consistency) that is permeable to the solvent (*e.g.* water) but relatively impermeable to the substances in solution, a passage of water tends to take place through the membrane from the weaker solution to the stronger. Membranes possessing this property are said to be *semi-permeable* with respect to the substance in solution. This attribute thus depends both upon the nature of the membrane itself and upon the solutions in relation to which it is used. The lining layer of protoplasm, or probably more correctly the plasmatic membranes, exhibit a varying degree of semi-permeability. Consequently, when cells are surrounded by solutions of substances to which the plasmatic membrane is relatively impermeable and which are more concentrated than the cell-sap, water passes out and the protoplast contracts. On the other hand, when replaced in water, the cell-sap is the more concentrated solution, and the protoplast becomes distended until its further expansion, and further increase in the volume of the sap, is limited by the stretching capacity of the cell-wall. In a healthy plant, supplied with sufficient water, all the living cells are thus distended, that is to say they are *turgid*, a condition which plays an important part in maintaining the stability of herbaceous organs.[1] Absorption of water by the cell also depends to a varying extent upon imbibition by the colloidal substances in the protoplast or cell-sap (cf. below, p. 72).

If cells were completely permeable, the concentrations inside and outside would rapidly become equal as a result of diffusion, and plasmolysis could not occur, nor would turgescence be possible. As a matter of fact, however, cells are relatively impermeable to many substances in solution, although when living cells are left immersed in a plasmolysing solution, the gradual recovery from plasmolysis which is observed in many cases, after a longer or shorter interval, shows that slow inward diffusion of the solute may occur. In some plants this is an important means of adjustment to changes of concentration in the soil-solution.

The plasmatic membranes exhibit their semi-permeable character, however, only so long as the protoplast remains alive; hence after death both the substances dissolved in the cell-sap can pass outwards, and external solutions can diffuse inwards. If cells of the Spiderwort, etc., mounted in water, are killed by gently heating the slide over a spirit-lamp, the coloured sap

[1] See p. 155.

will be found to escape into the surrounding liquid ; moreover, it will be found impossible to bring about plasmolysis or to render such killed cells turgid. These results, apart from showing that the semi-permeable character of the cytoplasm is altered by death, demonstrate that the cell-wall is permeable to substances in solution. The permeability of the cytoplasm, when dead, to the cell-sap may be exhibited on a large scale by placing slices of Beetroot in hot water.

A moment's thought, quite apart from any experimental demonstration, shows that the plasmatic membranes must be permeable to many substances, since most of those dissolved in the soil-water can be detected within the plant. Moreover, plants will thrive for months or years in a water-culture solution,[1] from which analysis shows that mineral salts have been absorbed (cf. also below, p. 68).

Were it not for the restraining influence of the wall, which is only slightly extensible, but possesses considerable strength, a plant-cell placed in pure water would increase in size until it became ruptured. This actually occurs when the root-hairs of salt-marsh plants are suddenly transferred to water, for these, like plants of dry situations, have a highly concentrated sap. The more concentrated the sap, the more strongly does it absorb water, and the greater will be the pressure exerted by the protoplast as it swells upon the wall. The maximum force with which a solution tends to take up pure water through a semi-permeable membrane is called the *osmotic pressure* of the solution.

The cell-sap has a variable osmotic concentration of molecules and ions which confers upon it a potential capacity to absorb pure water when separated from it by a semi-permeable membrane. When water is absorbed, the consequent swelling of the cell-contents causes an outwardly directed pressure (*turgor pressure*) to be exerted on the wall, which stretches the latter until the increasing pressure of the stretched wall (*wall pressure*) becomes great enough to resist any further increase in the volume of the cell-contents. So long as this limit is not reached, an isolated cell has a power to absorb water (*suction force* of the cell), which is equivalent to the difference between the force due to the osmotic concentration of the sap and the wall pressure. It is upon differ-

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[1] Cf. pp. 168, 169.

ences in suction force that exchange of water between adjacent living cells depends. At any time the intake of water by a cell of a tissue[1] depends on the difference between its absorbing force due to osmotic concentration and the forces tending to remove water from the cell, viz. (*a*) the pressure of the wall and that of the surrounding cells which oppose any increase in volume, and (*b*) the suction force exerted by the *other* living cells around which are also competing for water.

Loss of water from cells, as in transpiration, or gain in water, as in absorption by root-hairs, lead to alterations in the suction force of the cells concerned, and therefore establish gradients in suction force between these and neighbouring cells, by virtue of which movement of water from cell to cell and from one part of the plant to another takes place.

By using artificially prepared semi-permeable membranes the osmotic pressure of a solution can be determined and expressed in terms of atmospheric pressure. In general the osmotic strength of a solution depends upon the number of molecules it contains (though this does not apply to dilute solutions of many salts), so that when these are present in equal proportions, two solutions (*e.g.* of cane-sugar and grape-sugar) have the same osmotic pressure. Such *equimolecular* solutions are obtained by dissolving substances, in a litre of distilled water, in proportions equivalent to their molecular weights. If the number of grammes of the compound dissolved in a litre of water is equivalent to the molecular weight, we have a so-called molecular solution, briefly indicated by M. Solutions of other strengths are indicated as 0·5 M, 0.2 M, etc. Since the weight of a substance depends on the number and mass of the atoms composing its molecule, a 10 per cent. solution of a complex compound, such as inulin or dextrin, will contain fewer molecules than a 10 per cent. solution of a simpler compound, such as grape-sugar or cane-sugar ; moreover, cane-sugar, which has a higher molecular weight than grape-sugar, will exhibit a lower osmotic pressure than the latter when in solutions of the same *percentage* strength. These important facts are illustrated in the following table :

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[1] Even when a cell forms one of a tissue, it can receive water from all sides as long as the water-supply is normal, since all parts of a healthy plant imbibe water (cf. p. 72).

	Molecular weight.	Molar concentration of 10 per cent. solution.	Osmotic pressure in atmospheres.
Grape-sugar	180	0·555	12·43
Cane-sugar	342	0·292	6·54
Dextrin	—	—	ca. 2·2
Albumen	ca. 13,000	0·008	0·17

In order to estimate the osmotic pressure within a cell, a solution of sea-water (see Appendix III), strong enough to bring about plasmolysis, is first obtained. By experimenting with a series of solutions of diminishing strengths, one can eventually be found which just fails to cause plasmolysis, and which is slightly weaker than another which brings about a very slight contraction of the protoplast from the angles of the cell. The former solution gives the approximate osmotic concentration of the sap at the moment of plasmolysis. The value thus determined is somewhat higher than the osmotic concentration of the sap of the normal cell, owing to the contraction of the stretched wall and because water has been withdrawn during the experiment. It will, moreover, not be a true value unless the membranes can be assumed to be completely semi-permeable. More accurate determinations of the osmotic pressure of the cell-sap are made by indirect means, depending on the relation between osmotic pressure and the temperature at which a liquid (*e.g.* the expressed sap of a plant-organ) freezes.

In one and the same plant the osmotic concentration of the sap shows diurnal fluctuations and varies (sometimes as much as ten atmospheres in a day) with the humidity of the environment.[1] Very low values are characteristic of water-plants, whilst the highest osmotic concentration recorded is that of a desert plant, *Atriplex confertifolia*, in which 153 atmospheres may be realised.

The suction force of the cells of a plant is readily determined by the following method, depending upon the curvatures consequent upon the different stretching capacities of the walls of the component cells.[2] Short lengths of the stalk of a Dandelion-inflorescence, split lengthwise into four portions, are placed in water. Since the cells towards the outside of the stem have thicker walls than the inner ones, the latter have a greater aggre-

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[1] In *Helleborus fœtidus* osmotic pressures ranging from 10·5 to 66 atmospheres have been observed.

[2] Cf. also p. 156.

gate stretching capacity and the strips curl up and form rings. A strength of sea-water that causes neither increase nor decrease in the curvature will give an approximate measure of the suction force of the cells. Stems of many herbaceous plants can be utilised in this way.

The protoplast is very readily permeable to a number of organic substances, and these can be used to investigate this phenomenon. Thus, if young shoots of the Canadian Pondweed be placed in a solution of methyl blue, so weak that it has but a very faint tint, the cell-contents will after some days be found to have assumed a deep blue colour. This indicates that the dissolved dye has passed through the cytoplasm in considerable amount. If the methyl blue remained unaltered on reaching the vacuole, only sufficient could have entered to bring about a concentration equivalent to that of the solution outside the cells. But the deep blue colour shows that the dye has accumulated within the sap, and this is due to the combination of the methyl blue with the tannin in the latter to form a substance to which the plasmatic membrane is impermeable. In this way the concentration of the dye which enters the cell-sap is continually being reduced to a strength below that outside. As a consequence more and more methyl blue diffuses in, and thus the deep blue colour is gradually produced.

A further demonstration of permeability of the cytoplasm is obtained when filaments of *Spirogyra* (and many other Algæ) are placed in a dilute (1 per cent.) solution of caffein. Under the microscope, a very fine greyish precipitate is seen to appear in the vacuole, which, as it accumulates, renders the cell more and more opaque. This precipitate is again a consequence of combination between the tannin in the cell-sap and the caffein.

Both examples illustrate a very important phenomenon, viz. that plant-cells can absorb *and accumulate* considerable quantities of various substances *from very dilute solutions* by diffusion, provided that within the cell they are changed into some other form which is insoluble or does not readily pass through the plasmatic membrane, or that they are adsorbed (see p. 71) by colloidal substances. This fact is significant when it is remembered that many compounds are only present in the soil-water in very small amounts. The phenomena just discussed also explain the accumulation of food-reserves (*e.g.* insoluble starch) in large quantities in the cells of storage-organs. When these reserves are utilised, it is clear that they must be changed into a form which can diffuse to the growing organs, starch, for example, being transformed into sugar. This process can be simulated by placing leaves of the Canadian Pondweed, whose cell-sap has acquired a deep blue colour in the way above described, in a very dilute solution of citric acid (1 per cent.). The latter passes into the cells and changes the blue pigment into a form capable of diffusing through the plasmatic membrane. Since its concentration inside the cell is greatly in excess of that outside, diffusion takes place and the sap gradually loses its deep blue colouration.

Mineral salts, when used singly and in a sufficiently concentrated solution, may bring about contraction of the protoplast of plant-cells (*e.g.* root-hairs). It has been shown that many, and perhaps all, of these cases of so-called plasmolysis are due, not to impermeability of the plasmatic membrane to the substance in question, but to a poisonous or toxic effect of the latter upon the protoplasm. Two substances, however, which separately exert such a harmful effect can often, if mingled in appropriate proportions, provide a solution which produces no plasmolysis and is not poisonous. In the relatively dilute solutions of these compounds that are employed dissociation of the molecules into ions takes place, and the results just described are probably due to an effect of the metallic ions upon the proteins of the plasmatic membrane.

The prevention of the poisonous action of one ion by one or more other ions is spoken of as *antagonism*, and is probably greatest between ions of different valencies. A mixture of ions in solution in such proportions that they exert no toxic effect is called a *balanced solution*, and when a solution of this nature produces contraction of the protoplast, the effect is a true plasmolysis. In this category may be placed sea-water, which is a mixture consisting mainly of sodium chloride, magnesium chloride, magnesium sulphate, potassium chloride, and calcium chloride, and for this reason sea-water suitably diluted forms the best medium for determining osmotic pressures in the plant-cell.

The complexity of the phenomena of diffusion into the plant is illustrated by the fact that roots do not absorb compounds in the same proportions as they occur naturally in the soil-solution.

One of the most striking instances of such selective absorption is furnished by Seaweeds, which contain as much as 0·5 per cent. of iodine in their ash, whilst iodides are present in sea-water in almost imperceptible amount. Or again, silicates which are so very slightly soluble are taken up by Grasses in considerable quantities.

The diverse compounds occurring within the cells of plants, and continually being transported from one organ or tissue to another, are partly such as will diffuse readily through membranes (*crystalloids*) and partly such as are indiffusible (*colloids*). Examples of the former are afforded by mineral salts and sugars, and, of the latter, by gums and proteins. The difference between the two as regards diffusibility is so marked that mixtures of crystalloids and colloids in solution can be readily separated by dialysis, *i.e.* by placing the solution in a parchment tray floating on a large volume of water. In general crystalloids, in contradistinction to colloids, are substances which readily crystallise and which form true solutions. Under certain circumstances, however, many, and perhaps all, crystalloids can be caused to show certain of the characteristics of colloids. It is therefore more correct to speak of the colloidal state, in which many substances naturally occur, than to class colloids as a special group of substances.

The ordinary colloids can, by certain and varied treatment, be caused to form "solutions" which, however, differ from true solutions in being non-diffusible and in undergoing profound change on the addition of very small quantities of electrolytes. Similar "colloidal solutions," or *sols*, can be prepared from many crystalloids by appropriate means, and these show similar properties. A sol of the former type is obtained when boiling water is added to starch paste (p. 94), whilst a ferric hydroxide sol can be easily prepared by adding about 5 cc. of a 33 per cent. solution of ferric chloride to 500 cc. of boiling water.

In all true solutions one may assume that the molecules or ions of the dissolved substance occur independently of one another in the solvent. In the case of sols, however, the molecules are probably aggregated to form small groups which remain permanently suspended in the liquid, this continued suspension being dependent on electrical forces. In sols like those of the metals the particles in suspension are solid, and such sols grade imperceptibly into suspensions, such as that obtained when clay is shaken up with water. Other sols, however, contain liquid particles in suspension and are, therefore, of the nature of emulsions (*e.g.* oil in water, milk, latex). At the other extreme colloidal solutions grade over into true solutions.

The great characteristic of all sols, which distinguishes them from ordinary suspensions and emulsions, is the finely divided state of the particles. These latter can only be detected by the use of a special type of microscope, known as an ultramicroscope, and even then only in the case of those sols containing relatively coarse particles. When viewed by this instrument the particles do not appear stationary, but are seen to exhibit a constant oscillation which is due to surface action (cf. below). This movement, known as *Brownian movement*, is also recognisable under the ordinary microscope in all particles below a certain size.

By various means (change of temperature, addition of small traces of electrolytes, shaking, etc.) the particles in suspension in a sol are caused either to precipitate or the whole sol sets to form a jelly-like mass, or *gel*. The former result is obtained if a little sodium sulphate is added to the ferric hydroxide sol, whilst the latter is illustrated by the setting of solutions of gelatine or agar-agar, when cooled, or the coagulation of proteins (*e.g.* white of egg), when heated. In some, though by no means in all, cases these changes are reversible. It is very probable that the solid particles of the gels form a continuous phase, in the numerous interstices of which the water is held. The living protoplasm of the cell almost certainly has the structure of a gel and, like the latter, possesses the very important property of imbibing water. This property of gels is no doubt due to the large surface which they present; the amount of imbibition is, however, greatly influenced by the acid or alkaline reaction of the imbibing substance.

The individual molecules comprising the particles of a colloidal solution exert an attraction upon one another, but it will be obvious that, at the surface of each molecular aggregate, there is an unsatisfied molecular attraction which, though very limited in its sphere of action, is, within that sphere, very powerful. Consequently molecules of foreign substances which come within its domain may become attached to the surface of the molecular aggregates. This is probably the explanation of the phenomenon of *adsorption* which is very pronounced in gels and which finds expression in the capacity to take substances out of solution and to retain them very energetically.

Since the protoplasm of the living cell is a complex of colloidal substances it will, as already noted, imbibe water to the full extent and it is only under such circumstances that it is really in an active condition. It is, moreover, probable that many substances are retained in living cells by adsorption, without undergoing any chemical change, and that on the large surface afforded by the colloidal complex of the protoplasm many chemical reactions may take place between the adsorbed substances. When colloidal substances are transported from one part of the plant to the other they are, with certain exceptions (cf. p. 103), transformed into simpler ones capable of diffusion from cell to cell.

CHAPTER VII

GROWING POINTS AND CELL-DIVISION

IN some of the simpler forms of plants (*e.g. Spirogyra*) almost every cell may exhibit growth and division, but, in the vast majority, the cells originate in the first instance by division from so-called *growing points*. These, in the case of a flowering plant, are, as we have seen, situated at the tips of the stem and root and of their respective branches. A similar apical position of the growing point usually obtains amongst the lower plants.

In a flowering plant the growing point consists of a tissue of small actively growing and dividing elements, which takes the place of a single cell in many of the lower forms. Such a tissue is called a *meristem*, and is best examined by cutting longitudinal sections through the apex of stem or root. In both organs the cells are arranged in several layers (Fig. 34) which can be traced back into the different regions of the mature plant. As the cells of the growing point multiply, those that remain near the apex retain their power of division, whilst those that come to lie further back gradually pass over into permanent tissue.

In the stem the outermost layer of the meristem usually divides only by walls at right angles to the surface to produce a single layer of cells which becomes the *epidermis* (p. 127). The innermost cells derived from the growing point divide in all directions and can be traced back into the central region of the stem, which consists of *vascular strands* (p. 119) and pith. The middle layers of the meristem segment in like manner and develop into a part of the mature stem known as the *cortex* (p. 119). The growing point of the root (Fig. 34) is similar, except that segments are also cut off towards the outside to form the root-cap.

In the process of *cell-division* the nucleus always takes the lead, dividing into two parts, or daughter-nuclei, which become separated from one another by the development of an intervening wall. Thus two new cells are established, each with its own nucleus similar in all respects to that of the cell from which they originated. Amongst some of the lower plants, and as a rare phenomenon in the higher, the nucleus merely divides into two portions by a median constriction. This is spoken of as direct nuclear division (*amitosis*).

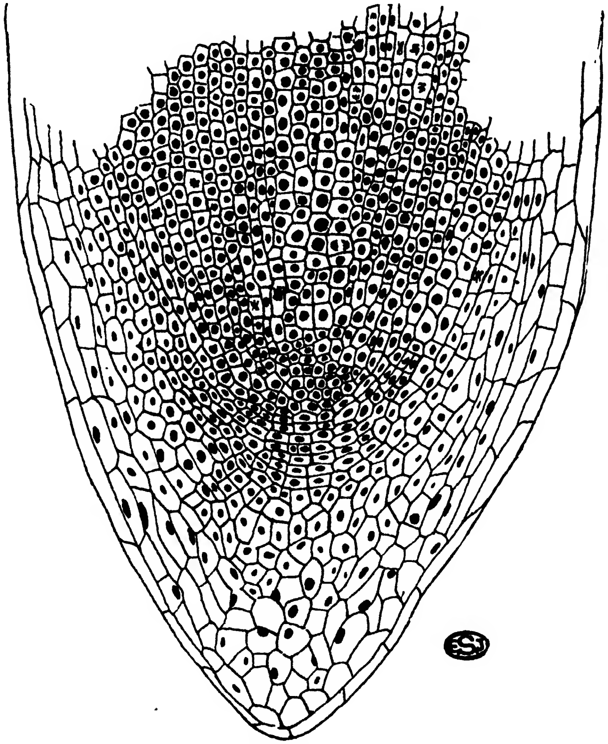

FIG. 34.—Root-tip of the Hyacinth (*Scilla*) in longitudinal section showing the growing point and the root-cap. Some of the nuclei (black) exhibit phases in nuclear division (cf. p. 76).

More usually, however, there is a sequence of complex changes in the nucleus preparatory to and during division, and this whole process is designated *mitosis* or indirect nuclear division.[1] All stages can be seen in a thin longitudinal section through the growing point of a higher plant (cf. Fig. 34); but in order to observe them readily, it is necessary to employ material which has been carefully preserved and suitably stained (see Appendix V).

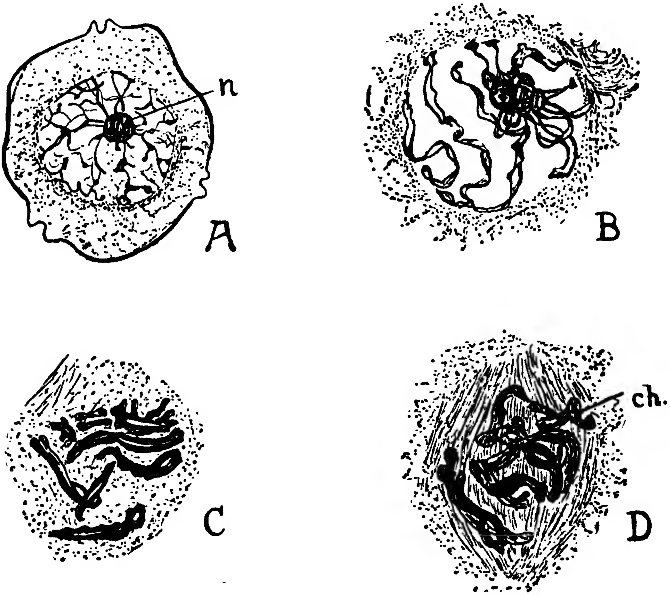

Fig. 35.—Early phases of mitosis (after Fraser and Snell). A, resting nucleus; B, spireme; C, formation of chromosomes; D, establishment of nuclear spindle. *ch.*, chromosomes; *n*, nucleolus.

The nucleus is usually oval in form (Figs. 30, N; 35, A), and, when not actually dividing, is spoken of as a *resting nucleus*, a term, however, which is apt to be misleading, since in this state it is probably just as active. Immediately within the nuclear membrane (p. 58) there is a more or less irregular network of deeply-stained substance, the *chromatin* (Fig. 35, A). The nucleoli (*n*), which are likewise deeply stained and consist of

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[1] The term *karyokinesis* is now rarely employed.

similar material, are situated just within this reticulum. The whole of the central region is occupied by the unstained *nuclear sap*, a denser peripheral portion of which contains the chromatin network.

The first change, indicating that division is about to occur, is a gradual simplification of the chromatin network, owing to the disappearance of some of the cross-connections and the closing up of some of the meshes. Later the chromatin network appears to consist of a number of irregular, ill-defined segments still exhibiting attachment to one another, especially near the ends. In the next stage, as a result of further concentration and disappearance of all except the terminal chromatin-connections, there remains a single thread exhibiting a split along its whole length, and irregularly coiled around the nucleolus or nucleoli (Fig. 35, B). This is known as the *spireme* stage.

Soon after this the nucleoli disappear, their chromatin probably having been absorbed into the thread. The latter now contracts somewhat, thus becoming thicker, and breaks up into segments or *chromosomes* (Fig. 35, C and D, *ch.*). The number of these has been found to be practically constant for the vegetative cells of any particular species.

Meanwhile the cytoplasm surrounding the nucleus becomes denser, and numerous streaks become apparent, radiating from each end of the cell towards the nucleus (Fig. 35, C, D), whose membrane has by this time practically disappeared. The radiating lines gradually extend into the central part of the nucleus and meet in its middle. They thus form a spindle-shaped group, termed the *nuclear spindle* (Figs. 35, D, and 36), the two points from which the individual streaks or *fibres* originate being called the *poles*. It is debatable whether the spindle fibres represent specialised strands of cytoplasm, or are merely the expression of physical forces operating within the cell.

Since the chromosomes result from the breaking up of a double thread, each is split longitudinally, but this is not always readily recognisable at this stage. The chromosomes now become grouped in the equatorial region of the nuclear spindle, and seem to become attached to some of its fibres (Fig. 36, A). In the next stage these apparently shorten, and the two halves of each chromosome become separated (Fig. 36, B), and begin to move towards the opposite poles, which they ultimately reach (Fig. 37, A). The diverging pairs of chromosomes often form loops or V's, according to the mode of attachment to the spindle, and during their passage to the poles each frequently exhibits a longitudinal split comparable to that present in the parent-chromosome. This split probably forms the plane of separation of the two halves at the next nuclear division.

On reaching the poles the chromosomes give rise to two daughter-nuclei (Fig. 37, B), which pass into the so-called resting-stage by a series of changes broadly the reverse of those taking place at the commencement of nuclear division. That is, the individuality of the chromosomes becomes obscured, owing to the formation of numerous cross-connections between them and to partial separation of the two halves of each chromosome, which only remain joined at the ends and by fine processes in between. With the appearance of nucleoli and a new nuclear membrane, the resting nucleus with its chromatin-reticulum is again established.

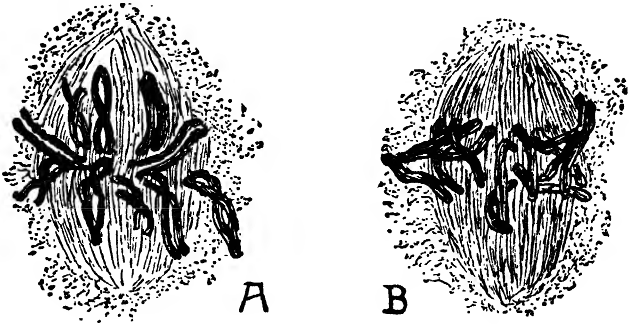

FIG. 36.—Mitosis (after Fraser and Snell). A, equatorial grouping of chromosomes. B, separation of split halves. Chromosomes are shaded.

From the original nucleus two daughter-nuclei are hence formed, either of which contains a half of each of the chromosomes of the parent-nucleus. As the process is repeated at every division, all the vegetative cells[1] of the plant come to possess nuclei with the same number of chromatin-masses.

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[1] For details of nuclear division in reproductive cells, see p. 273.

In addition to the contractile fibres which were attached to the chromosomes, other fibres extend through the cytoplasm from pole to pole. These persist for some little time after the establishment of the daughter-nuclei, and develop thickenings in the equatorial plane, an appearance probably due to a modification of the cytoplasm in this region. These thickenings become more conspicuous as they extend horizontally across the parent-cell, till finally they join to form a complete diaphragm of modified cytoplasm, the *cell-plate* (Fig. 37, B). Within the latter there is formed a thin membrane of cell-wall substance which separates the two daughter-cells, and is traversed by the fine cytoplasmic connections representing the fibres. The latter persist, even in the adult condition, so that the protoplasts of adjacent cells of most plants are connected by living matter. Subsequently further layers, consisting largely of cellulose, are deposited on either side of the original membrane, which is the only part of this separating wall common to the two daughter-cells. These additional layers frequently become chemically changed in various ways, but the original separating wall, termed the *middle lamella* (Figs. 39, 40, *m.l.*), does not usually undergo such profound modification, so that it is readily dis-

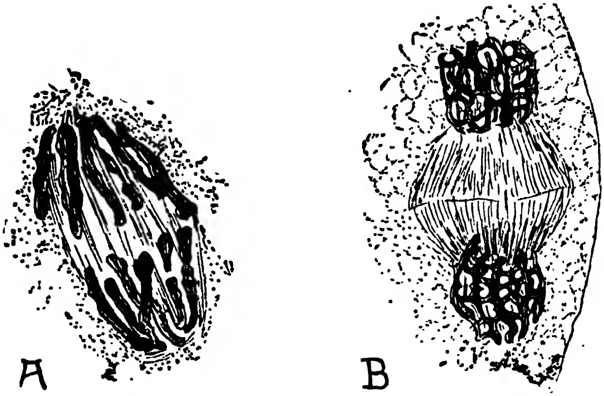

Fig. 37.—Mitosis (after Fraser and Snell). A, chromosomes have separated and reached the poles. B, establishment of daughter-nuclei and development of cell-plate.

tinguished by its different density, and often stains more deeply.[1] The further modification of the cell-wall will be dealt with in the next chapter.

From the foregoing it is evident that, when cell-division takes place, the nuclei of the daughter-cells are derived from that of the parent-cell. This fact holds generally throughout the Vegetable and Animal Kingdoms, the nucleus of any given cell always being the product of a pre-existing one. The origin of a new nucleus from the cytoplasm is unknown. In like manner it is probable that chloroplasts (and other plastids) multiply by division and are derived from pre-existing specialised cytoplasmic bodies. During the enlargement usually following upon cell-division considerable increase of the cytoplasm may take place; but it should be emphasised that new protoplasm is only formed in connection with a pre-existing protoplast, the independent origin of living matter being unknown. In other words, both in the Animal and Vegetable Kingdoms, one generation is merely a continuation of the previous one, the reproductive cells of any one dividing and enlarging to form the body of the next.

We can now consider how the cells produced at the growing point gradually pass over into the mature condition. Just below the apex they have dense cytoplasmic contents, are more or less rectangular or polygonal, and fit closely together, without any interspaces. A little further back, representing an older phase, they increase appreciably in size and often become more or less rounded off, as a result of which small spaces, the *intercellular spaces* (Fig. 52, *i.p.*), appear between them, particularly at the angles.

The increase in volume of the cells is almost entirely due to the intake of water which results from the formation of substances that bring about an increase in osmotic pressure. These substances are produced during the living processes carried on in the cells, and, as a consequence of their solution, a number of small vacuoles containing cell-sap appear in the cytoplasm. These vacuoles gradually increase in size, and ultimately coalesce to form one (*e.g.* Onion, Fig. 30) or few large vacuoles. Apart from its presence in the vacuoles, however, water also permeates

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[1] The separating wall in many Algæ arises as an ingrowing diaphragm, and this is not always directly related to nuclear division.

the protoplasm and cell-wall, forming the so-called *imbibition-water* (cf. p. 72).

A type of growth not infrequent in developing tissues is that in which the elongating cells produced by division slide by one another as they increase in size (*gliding growth*).

With the gradual assumption of the mature condition the cells generally lose their power of division, though this faculty may be again stimulated into activity, as when a plant is wounded. The growth of any organ of the plant is thus mainly the outcome of multiplication of cells at its growing point, their subsequent increase in volume leading both to a lengthening and gradual widening of the tissues. As they reach maturity the new units mostly become specialised in various directions to serve diverse needs. Those, however, which have not undergone profound alteration, but have retained their juvenile character, often retain also their power of division and capacity to develop in different ways as the demands of the organism may dictate. It is the visible enlargement of plants that is popularly spoken of as growth, but in reality this involves the three phases of cell-division, enlargement, and the final differentiation which will form the subject-matter of the next chapter.

CHAPTER VIII

THE DIFFERENTIATION OF PLANT-CELLS

FOUR principal types of element [1] are found in vegetable tissues. A large part of the plant-body is composed of cells which usually appear rounded or polygonal in transverse sections, and in most cases contain a living protoplast. In longitudinal sections they are often rectangular in form, seldom more than two or three times as long as broad, and provided with square or rounded ends (cf. Fig. 58, p. 124). Such cells, described as *parenchymatous*, frequently have thin walls, and often form an extensive tissue known as *parenchyma*.

In contrast to this type are other cells, termed *prosenchymatous*, in which the length greatly exceeds the breadth, such elements being found more particularly in the mechanical and conducting tissues. These cells usually have pointed ends and thickened walls (Fig. 41, C, D), and the width, as seen in transverse section, is commonly small as compared with that of a parenchymatous element (Fig. 41, B). Occasionally forms of cells are encountered which are transitional between these two types.

The elements of the third type are of quite a different character, and are termed *vessels* (Fig. 42). They are the principal water-conducting structures in the wood of Flowering Plants, possess no living contents when mature, and their longitudinal walls are thickened in the various ways to be described below

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[1] These, and the various modifications described in the present chapter, are most easily studied by teasing out (*i.e.* tearing to pieces with a pair of needles) small portions of a Celery-stalk or Marrow-stem that have been previously boiled for some time in water; the middle lamellæ are thereby dissolved, so that the individual cells readily separate from one another.

(p. 89). In the mature condition they appear as long wide tubes or cylinders, but they are actually derived from vertical rows of cells by the more or less complete breaking down of the cross-walls. Perforated septa thus occur at intervals in the course of the vessel, and in woody plants are often obliquely radial with reference to the organ as a whole. The cross-walls may almost entirely disappear (as in the Maple and Oak, Fig. 42, F), but most commonly a distinct rim persists, only the central part being absorbed (*e.g.* the Lime or the Poplar, Fig. 42, E). In still other cases the walls break down in such a way that a number of cross-bars remain (*e.g.* the Alder, Fig. 42, D).

The elements of the fourth type likewise serve for conduction, in this case of elaborated food-materials. They are known as *sieve-tubes*,[1] and are located in the bast or phloem, a tissue that in most stems lies just outside the wood. The sieve-tubes, like the vessels, are derived from vertical rows of cells whose cross-walls are perforated by a large number of fine pores through which the protoplasts of the adjacent units become connected. They retain their living contents in the mature condition, and the membranes remain relatively thin (Fig. 38). When the cross-walls are seen from the surface they present the appearance of a sieve, the meshes of which constitute the pores ; these walls are spoken of as *sieve-plates* (Fig. 38, *s.p.*).

Before the sieve-plates are fully developed each cell divides longitudinally into two unequal portions. The larger constitutes a segment of the sieve-tube whose nucleus is stated generally to degenerate, whilst the smaller, which retains its nucleus, forms a so-called *companion cell* (Fig. 38, *c.c.*). In some cases two, or even three, companion cells may be produced before the nucleus of the sieve-tube segment dies away. The narrow companion cells have dense granular contents in contrast to the wider sieve-tubes, which possess but a thin lining layer of cytoplasm and a large central vacuole, features by which they are often readily recognised in transverse sections.

Behind the growing point the cells have been seen to exhibit a steady increase in size until they attain their full dimensions. During the phase of enlargement the walls undergo no appreciable

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[1] See also p. 123.

thickening, but surface growth takes place. This is probably accomplished by stretching of the elastic membrane and intercalation of new particles of cell-wall substance between those already present. When fully grown more or less marked *thickening of the wall* occurs, successive layers formed by the agency of the living protoplast being deposited on the inner surface. Subsequently the wall often undergoes considerable chemical changes, as a result of which it may become more or less impermeable to water, so that the contained protoplast dies. When the thickening is at all conspicuous, the successive layers generally appear more or less distinct (Fig. 39, D; 41, B). This *stratification* is due to the fact that the layers adjacent to one another are of unequal density, so that one is more transparent and consequently brighter than another.

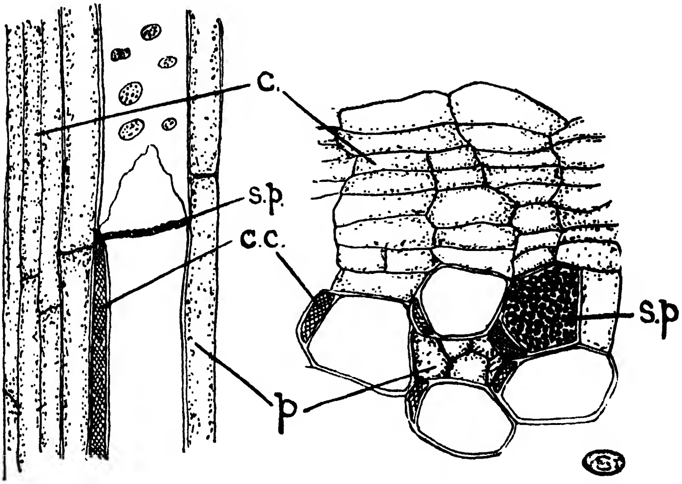

FIG. 38.—Phloem-structure of the Vegetable Marrow (*Cucurbita*) in longitudinal (left) and transverse (right) sections. *c.*, cambium; *c.c.*, companion cells; *p*, phloem parenchyma; *s.p.*, sieve-plate.

As a general rule the thickening is not uniform over the whole inner surface of the wall, small areas commonly remaining thin (Fig. 39, A, B). The intimate relation between adjacent cells is evidenced by the fact that such thin areas, interrupting the layers formed by the protoplast of one cell, coincide with the thin areas on the outer sides of its walls, where the thickening has been deposited by the protoplasts of the surrounding cells. At these points, known as *simple pits*, the original middle lamella (the *pit-membrane*, Fig. 39, A, *pm.*) alone separates the adjacent cells. In these cases the bulk of the protoplasmic connections (cf. p. 78) pass through the pit-membrane.

Good examples of simple pits are seen in sections of Elder pith (Fig. 39, B). In surface view they appear as irregularly scattered oval or elliptical areas which are more transparent

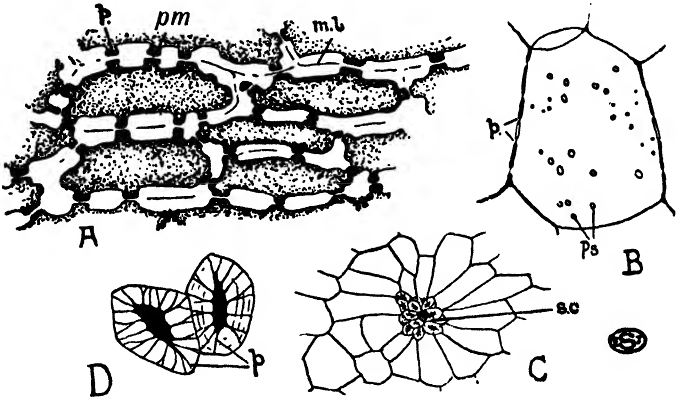

Fig. 39.—Thickened cell-walls. A, Portion of the endosperm of the Date in section. B, Pith-cell of the Elder. C, A group of stone-cells of the Pear, together with a small part of the adjacent flesh. D, Two isolated stone-cells. *m.l.*, middle lamella; *p.*, pits seen in section; *pm.*, pit-membrane; *Ps.*, pits in surface view; *s.c.*, stone-cells.

than the rest (*Ps.*). In section (*p.*) the walls appear broken at sundry points; but careful focussing shows that the apparent gaps are really bridged by a thin line, the pit-membrane. In certain cases [*e.g.* the endosperm of the Date (Fig. 39, A), the cotyledon-walls of the Lupine and many other Leguminosæ, and cells of the cortex of the Mistletoe] the thickening is so extreme that the cavity of the cell becomes much reduced, and the pits then appear as deep depressions within the wall. It is in such tissues that the protoplasmic connections between cell and cell can most readily be demonstrated.

The thick-walled elements of the plant are of considerable mechanical importance, since they form skeletal tissues which are mostly devoid of intercellular spaces. When such mechanical elements occur in young growing organs, where too great a rigidity is disadvantageous, they take the form of *collenchyma*, which differs from other strengthening tissues in the fact that its cells are living. Collenchyma is frequent immediately beneath the epidermis in young stems (Fig. 55, *s*), in the midribs of young leaves (Fig. 65, M), and in the adult stems of some herbs (*e.g.* Hogweed). In its most typical form it is characterised by extreme thickening of the corners of the cells, as seen in transverse section (Fig. 40), the thickened angles appearing bright and shining owing to their highly refractive character. Sometimes, however, collenchyma exhibits uniformly thickened walls, interrupted only by pits. The thickening, unlike that of most mechanical elements, is practically unaltered *cellulose*, which possesses considerable stretching power, so that collenchyma is well suited to act as a supporting tissue in young growing organs.

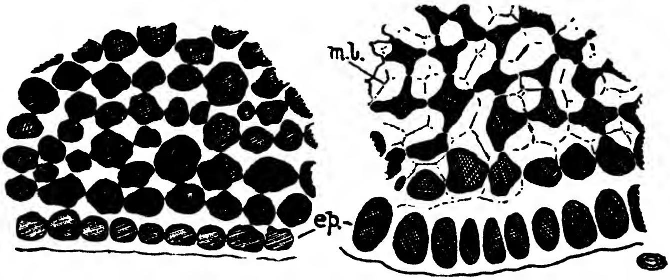

FIG. 40.—Collenchymatous tissue from the stems of the Burdock (*Arctium*) (left) and Dead Nettle (*Lamium*) (right). *ep.*, epidermis ; *m.l.*, middle lamella. Both in transverse section. The cell-contents are shaded.

All cellulose-walls[1] exhibit this character, and, moreover, are readily permeable to water. Cellulose is one of the more complex carbohydrates, belonging to the series of the polysaccharides, and composed of a large number of $C_6H_{10}O_5$ groups. It is scarcely coloured by iodine solution, but is stained blue

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[1] Mingled with the cellulose in the walls of many plant-cells, especially those of succulent fruits (*e.g.* Apples, Gooseberries) and storage roots (*e.g.* Beetroot), are so-called pectic substances which are soluble in water.

if the application of iodine is followed by that of strong sulphuric acid. The acid causes swelling of the wall, and this is followed by complete solution, the blue colour with iodine being due to one of the products. Cellulose-walls are likewise dissolved by ammoniated copper oxide (cuprammonia, see Appendix I). A blue colouration and swelling also results from the application of chlor-zinc-iodide (Schultze's solution, Appendix I), but it is necessary to use the freshly made compound, as it soon decomposes. For general purposes useful stains for cellulose-walls are methyl blue and hæmatoxylin (Appendix V), the latter giving a deep purple colour.

The remaining mechanical elements form tissues termed *sclerenchyma* and distinguished from collenchyma by a chemical change of the thickened walls known as *lignification,* in consequence of which the cell-contents ultimately die. Such lignified walls are much harder and stronger than those consisting of cellulose, features which are the cause of the toughness of wood. They possess relatively little elasticity, and when wet are not readily permeable to water and practically impermeable to air. The exact nature of the chemical change is not known, but it is sufficiently profound to lead to marked differences in reaction. Thus such walls are insoluble in cuprammonia, whilst the lignin is dissolved by Eau de Javelle (Appendix I). Iodine solution stains lignified walls brown, and a similar colouration is obtained with chlor-zinc-iodide. Aniline chloride, or sulphate, which does not affect cellulose-walls, yields a brilliant yellow colouration and, as it does not stain starch, is particularly useful when that substance is present in quantity. An alcoholic solution of phloroglucin, followed by strong hydrochloric acid, produces a scarlet colouration. Lignified walls stain yellow or brown with hæmatoxylin, and are deeply stained by gentian violet. The latter is most effective in conjunction with Bismarck brown, the wood and other sclerenchyma becoming violet and the ordinary cell-walls brown.

There are two principal types of sclerenchymatous elements, viz. stone-cells and fibres; of these the former are more or less parenchymatous, the latter prosenchymatous in shape. The gritty character of the flesh of the Pear is due to *stone-cells* which, in a thin section, will be found to occur as little clusters

(Fig. 39, C) irregularly scattered through the thin-walled parenchyma forming the flesh. The cavity of each stone-cell is very much reduced and inconspicuous owing to the strong thickening of the wall (Fig. 39, C and D, *s.c.*). This shows distinct stratification, and is traversed by a number of dark lines (*p.*) radiating from the centre and branching as they approach the surface. These are the pits (spoken of as *pit-canals* when they exhibit this narrow elongated form) which serve for the transference of nourishment to the protoplast during the process of thickening, on the completion of which the living matter dies.

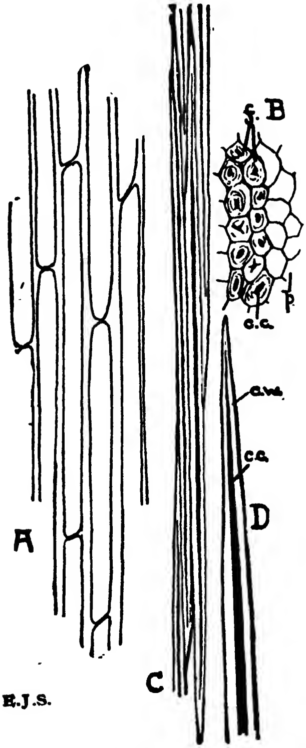

FIG. 41.—Collenchyma of Dead Nettle stem in longitudinal section (A), and fibres from the stem of the Hop in transverse (B) and longitudinal sections (C, D). *c.c.*, cell cavity; *c.w.*, cell-wall; *f*, fibres; *p*, parenchyma.

The *fibre* is a narrow, very much elongated, cell with tapering pointed ends, and in the adult condition its protoplast is frequently dead. The walls are in general strongly thickened and lignified (Fig. 41, B–D), and usually bear a number of oblique slit-shaped pits. In the mature plant fibres are generally the most important form of mechanical element, and compose a large proportion of the wood of thicker branches (cf. p. 144); these *wood-fibres* sometimes bear a modified type of bordered pit (see below). The cortex in the young stems of many woody plants exhibits a continuous mechanical ring composed of alternating groups of fibres and stone-cells.

Plant-fibres can undergo considerable elongation and can bear very heavy strains without losing the power of again contracting to their original length; as a matter of fact, loads varying from 14 to 25 kilogrammes are required to produce permanent lengthening. The powers of fibres in this respect may be compared with those of metal rods (*e.g.* of wrought iron and steel) which, whilst they become permanently stretched under similar strains, exhibit far less extension before the limit of their elasticity is reached. Fibres will thus permit bending on the part of a plant-organ (under the influence of the wind, for example), and will not give way, even under considerable strain; moreover, their elasticity will bring about a return to the normal position as soon as the strain is relieved. Whilst the breaking strain (10–12 kilogrammes) for collenchyma is not much less than that for many fibres, it exhibits permanent elongation under quite low tension, so that it is especially suited to the mechanical needs of a growing organ where constant extension is taking place.

The main function of *vessels* (Fig. 42) is water-conduction, but they also are elements of mechanical importance on account of their thick walls. The type of thickening varies greatly, depending largely on whether the vessel is formed in a part of the plant that is still growing or in one that has reached maturity. In the former case the thickening must be of such a nature as to admit of stretching of the wall, which would otherwise be ruptured.

The first-formed vessels of the wood, which differentiate a short distance behind the growing point, exhibit continuous spirals or disconnected rings of thickening (*spiral* and *annular* vessels, Fig. 42, A, B), deposited on the inner side of the original vessel wall. As the organ elongates the spirals are drawn out like a spring, and the rings become more widely separated, by the gradual stretching of the unthickened part of the wall. If, however, growth in length is very considerable (as, for instance, in many Monocotyledons), complete rupture may ultimately take place, so that in the mature plant only an irregular canal remains to indicate where the first-formed vessels were situated.

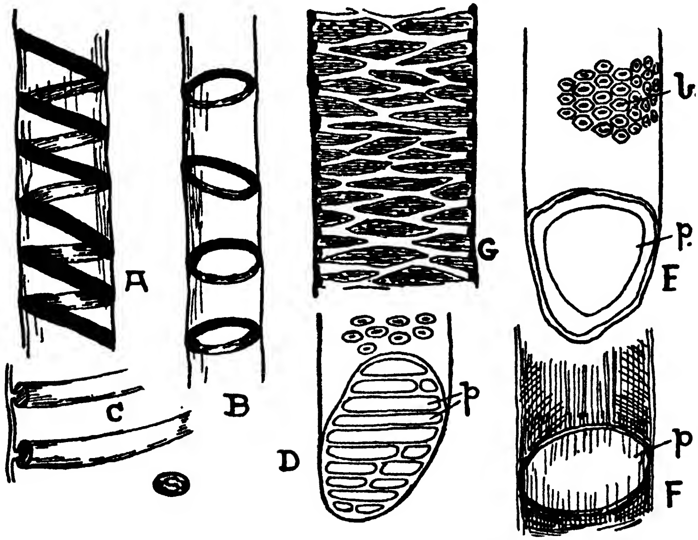

FIG. 42.—Vessels showing various types of thickening and perforation. A, spiral; B, annular; C, portion of A in longitudinal section showing attachment of thickening to wall; D, end of vessel of Alder (*Alnus*) showing ladder-like perforation; E, vessel of Poplar (*Populus*); F, vessel of Oak (*Quercus*); G, reticulate vessel of Marrow (*Cucurbita*). *b*., bordered pit; *p*., perforations between segments of vessel.

The vessels formed after completion of growth often exhibit *reticulate* thickening (Fig. 42, G), which appears as a more or less irregular network of ridges deposited on the inner side of the original wall. In many cases careful examination shows that the meshes of this reticulum possess the characters of the bordered pits about to be described.

Such *bordered pits* are very common on the vessels in the older wood. An examination of the surface of the vessel wall under the high power of the microscope shows that each pit is provided with a broad *border* (Fig. 42, E, *b*.). In section the latter is recognised as a dome-shaped cover formed by the thickening of the wall, which around the pit arches away from the middle lamella (*i.e.* pit-membrane); the top of this low dome is perforated by the aperture leading into the pit. Where two vessels adjoin one another, such a perforated dome occurs on either side of the common wall, so that these bordered pits coincide.

The walls of mature cells often undergo chemical changes other than lignification, some of which (*e.g.* the change affecting the cells of the cork, p. 151) will be described later. In a number of cases the thickening of the walls of certain cells takes the form of layers of *mucilage* (*e.g.* Seaweeds). The *gums* (gum arabic, gum tragacanth) formed by certain plants are probably very similar chemically, and appear, in many cases at least, to arise as a result of alteration of the cell-wall.

CHAPTER IX

The Non-living Contents of Cells

Apart from the living constituents, cells usually contain numerous substances which are either dissolved in the sap or, when insoluble, occur as solid bodies or suspended drops. These substances can for the most part be grouped as food-bodies or as by-products, according as they are known to be employed in the nutrition of the plant or are believed to be of no further nutritive value.

Among the commoner *food-substances* are various carbohydrates (*e.g.* sugars, starch, etc.), oils, and proteins, all of which are built up from simple inorganic compounds (cf. p. 11) by a series of complex changes. During the earlier part of the season such food-substances are used directly to supply the necessary materials for growth, but subsequently, with decreasing demands, a large proportion are stored up for future use. In perennial plants they accumulate in those organs which persist from year to year (*e.g.* bulbs, tubers, etc., and, in the case of woody perennials, the stem- and root-systems).[1] Similar food-substances are, moreover, laid up within the cotyledons or endosperm of all seeds.

One of the most important food-substances is *starch*, which is insoluble. We have seen that it is often the first easily recognisable product of photosynthesis in a green leaf which has been exposed to light. On microscopic examination the starch appears as very small shining grains, mainly within the chloroplasts (Fig. 32, *St.*). These grains gradually increase in amount during the day, but generally disappear over-night, and are consequently spoken of as *transitory starch*. Their gradual

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[1] Cf. pp. 17, 179.

accumulation on a bright day is due to the conversion of the soluble carbohydrates (*e.g.* sugars), which are produced more rapidly than they can be removed, into insoluble starch. In darkness, when carbon dioxide assimilation ceases, the accumulated starch is changed back into sugar and transferred to other parts of the plant.

In contradistinction to this transitory starch, that which accumulates in storage-organs usually takes the form of rather large grains which originate within colourless plastids, known as *leucoplasts*. The latter occur in those cells which are not exposed to light, and differ from chloroplasts only in the absence of chlorophyll, which is generally not produced in darkness. Leucoplasts, however, readily change to chloroplasts. When a Potato-tuber, for instance, is exposed to light, it turns green through the formation of chlorophyll within the leucoplasts. In a few cases large starch-grains are actually produced within green plastids (*e.g.* in a small greenhouse plant known as *Pellionia*), and these provide particularly appropriate material for studying the mode of formation of the grains.

Thus, in a transverse section of the stem of *Pellionia* the outermost cells (Fig. 43, *a*) are seen to contain chloroplasts (*ch.*), in some of which there is a bright shining dot, the transitory starch-grain (*s*). The larger starch-grains, seen nearer the centre in various stages of development, may be supposed to have originated likewise, as small bodies within the chloroplasts there situated (Fig. 43, *b*). But in the mature condition these grains have enlarged to such an extent that the enveloping chloroplasts appear merely as green caps to one side of them (Fig. 43, *c*). On staining with dilute Iodine both small and large grains take on the blue colouration typical of starch.

The large starch-grains that can be scraped out of a Potato are more suitable for the study of details of structure. Examined in a drop of water, each shows a number of asymmetrical layers arranged concentrically around the darker *hilum*, or point of origin (Fig. 43, *d*). This stratification indicates the manner of growth of the starch-grain, the successive layers being distinguished, presumably, by differences either in chemical or physical structure. In the grains of the Potato (Fig. 43, *d*) and *Pellionia* (Fig. 43, *c*) the point of origin is towards one end (*excentric* type).

On the other hand, the hilum, in those from the cotyledons of the Pea or Bean, lies in the centre (*centric* type, Fig. 43, *f* and *g*), and the layers are arranged symmetrically around it. The

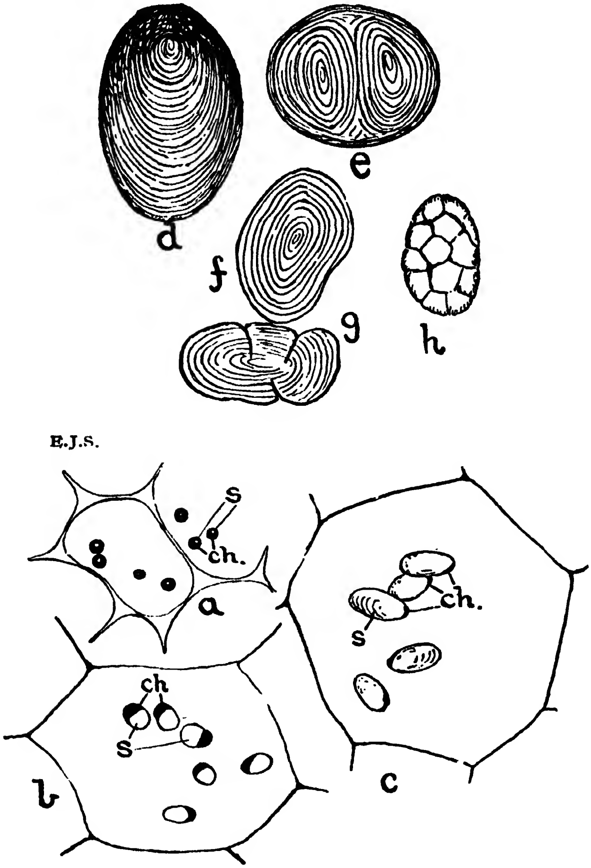

FIG. 43.—Starch-grains. *a–c*, stages in the development of grains within the chloroplasts of *Pellionia*; chloroplasts black, starch-grains white; *ch.*, chloroplasts; *s*. starch-grains; *d* and *e*, Potato starch; *f* and *g*, Pea starch; *h*, compound starch-grain of Rice.

dry grains of Pea, Bean, etc., exhibit a number of radiating cracks, which appear as dark irregular lines (Fig. 43, *g*); these seem to be due to the drying up of some of the imbibed water which permeates the substance of all starch-grains.

Whilst most of the grains of Potato-starch show but a single hilum, an occasional one will be found to possess two or three, each with its own system of layers (Fig. 43, *e*). This results from the development of several grains within the same leucoplast, growth of each occurring independently until they meet; in some cases deposition of starch continues with the formation of layers common to the whole group (Fig. 43, *e*). Such structures are called *compound grains*. In some plants (*e.g.* in many cereals) numerous grains arise in each leucoplast, so that the compound structure may consist of a thousand or more units. Thus a starch-grain of the Rice (Fig. 43, *h*) or Oat is marked out into a number of small areas, each representing a constituent unit.

Starch-grains consist of at least two substances, an outer layer composed of amylopectin and an inner layer consisting of the polysaccharide (cf. p. 85) amylose; these occur approximately in the proportions of two to one. The two constituents may be separated by the treatment of starch with dilute caustic soda or by the action of enzymes. Amylopectin is composed of a carbohydrate-complex in combination with phosphoric acid, whilst amylose is a pure carbohydrate. When boiled with water, starch-grains swell and provide a starch-paste or " starch-solution," which is considered to be a solution of amylose thickened by a gelatinous suspension of amylopectin. This " solution " is colloidal in character, and therefore will not diffuse through an organic membrane. Examination with X-rays appears to indicate that starch-grains have a crystalline structure. Under polarised light they exhibit a black cross with the hilum as its centre.

The accumulation of starch-reserves by plants is a feature of the greatest economic importance, constituting as they do a very important article of human diet. The cereals, the pulses, and Potatoes, all of which contain a high percentage of starch (cf. p. 104), furnish a sufficient illustration. Rice, which perhaps constitutes the most widely consumed food in the world, is the grain of *Oryza sativa*, a Grass cultivated in most parts of the Tropics where the necessary water for submerging the rice-fields is available. Tapioca is obtained from the root-tubers of the Cassava or Mandioc (*Manihot utilissima*, widely grown in the Tropics), whilst sago is the starch found in the pith of various

Palms (mainly species of *Metroxylon*, cultivated in the Malay region), from which it is extracted after the appearance of the inflorescence.

The wide distribution of starch as a form of storage of carbohydrate material can probably be related to its insoluble character, in consequence of which it exerts no osmotic pressure. The small amount of moisture in seeds renders them unsuited to the storage of soluble carbohydrates, and doubtless explains the frequent occurrence of starch in the endosperm and cotyledons. In succulent storage organs, on the other hand, soluble carbohydrates often occur. One of the most important is *inulin*, another of the complex polysaccharides, though with a molecular weight smaller than that of starch. As a result, in spite of its solubility and frequent high concentration, inulin has but little effect on the osmotic pressure of the cells containing it (cf. p. 65).

Inulin is found especially in the Compositæ and the allied family of the Campanulaceæ, but also in the bulb of the Wild Hyacinth (*Scilla nutans*) and in other Monocotyledons. Soluble carbohydrates of a similar chemical constitution are, moreover, encountered in many members of the latter group (*e.g.* the graminin of Grasses, the irisin of the Iris, etc.).

In a fresh Dahlia-tuber, in a Salsify-root, or in a tuber of the Jerusalem Artichoke, the intact parenchymatous cells contain inulin dissolved in the sap. On placing relatively thick sections in spirit, the inulin is deposited as a finely granular precipitate. In sections of material kept for some weeks in spirit, so that the latter has only penetrated slowly into the tissues, the inulin will be found as big spherical or lobed masses deposited on the cell-walls. These *sphere-crystals* (Fig. 44, *In.*) usually show concentric layers, whilst radial lines traversing them indicate the numerous needle-like units of which they are built up. On warming in water, the precipitates and sphere-crystals of inulin readily dissolve. Sections treated with orcin (in alcohol), followed by concentrated sulphuric acid, acquire a deep orange-red colour.

Sugars are among the most important of the soluble carbohydrates present in plants. They possess much simpler molecules than the polysaccharides just considered, being either monosaccharides with the general formula $C_6H_{12}O_6$, or disaccharides with the formula $C_{12}H_{22}O_{11}$. Disaccharides and polysaccharides are so called since they respectively split up, under certain circumstances, into two or many molecules of monosaccharides.

Among the *monosaccharides* found in plants, the commonest are dextrose or glucose (popularly known as grape-sugar) and fructose or levulose (fruit-sugar), whilst of the *disaccharides* sucrose or saccharose (cane-sugar) and maltose (malt-sugar) deserve mention. Owing to their simple molecules they produce a relatively high osmotic pressure, although for solutions of equal strength this is greater in the case of the monosaccharides than in that of the disaccharides. For this reason no doubt grape-sugar and cane-sugar, the two which function as food-reserves, are only found in very minute quantities in seeds (except for the cane-sugar in the Sweet Corn, a variety of Maize). On the other hand, grape-sugar is one of the principal carbohydrate-reserves in the bulb of the Onion, whilst cane-sugar occurs in the Sugar Beet (*Beta*), in the pith of the stem of the Sugar Cane (*Saccharum officinarum*), and in the Sugar Maple (*Acer saccharinum*, N. America). The sugar is extracted from the sliced Beet with the aid of warm water, whilst in the case

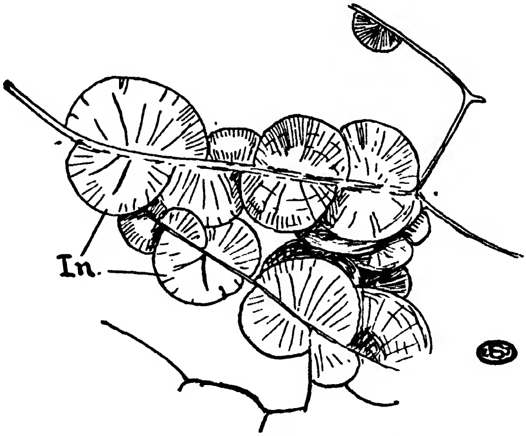

Fig. 44.—Sphere-crystals of inulin (*In.*) in the cells of the tuberous root of a Dahlia.

of the Sugar Cane the juice is crushed out of the canes with the help of rollers. In all cases the crude sugar is subjected to subsequent processes of refinement.

Fructose is most abundant in succulent fruits, and is an important constituent of honey; in both, however, it is mixed with, usually smaller amounts of, grape and cane sugars. In such cases, however, the sugars are not of the nature of food-reserves, but serve a biological purpose in connection with seed-dispersal and cross-pollination (p. 287).

All the four sugars above mentioned are found in foliage-leaves, though in proportions that vary greatly both during the day and night and at different seasons of the year. It is still an open question whether glucose or sucrose is the first sugar to be formed in photosynthesis; but there is no doubt that the other two, like the transitory starch, are secondary products. *Maltose* appears to be produced invariably during the solution of starch within the plant, and is consequently found not only in foliage-leaves, but in germinating Barley (malt) and other starch-containing seeds. The fructose found in leaves, on the other hand, is formed by the breakdown of cane-sugar.

The latter is readily split (in the presence of water, so-called hydrolysis) into two molecules of monosaccharide by boiling the solution with a few drops of some mineral acid (*e.g.* hydrochloric acid) ; one molecule of glucose and one of fructose are obtained, a mixture known as *invert sugar*. Cane-sugar is similarly decomposed by *invertase*, one of the so-called enzymes (cf. p. 183), which is found in most plants. In the same way the polysaccharides above discussed can be split up with the formation of disaccharides or monosaccharides, as the case may be. For instance, a starch "solution" boiled with a few drops of a mineral acid becomes clearer, and the ordinary reaction to iodine gradually disappears ; the colour assumed with this reagent is now reddish, owing to the presence of simpler polysaccharides known as *dextrins*. If the boiling be continued, the whole of the starch "solution" ultimately breaks down into simple glucose. Similarly inulin gives rise to fructose. In the plant starch and inulin are acted upon by the ferments *diastase* and *inulase* (p. 183), which effect like changes, except that diastase breaks down starch into the disaccharide maltose, which in its turn is acted upon by an enzyme *maltase* with the production of two molecules of glucose.

The sugars are readily distinguished from one another by certain characteristic reactions. Thus glucose, fructose, and maltose all reduce Fehling's solution (which contains cupric oxide, Appendix I) with the formation of a red precipitate of cuprous oxide, and are consequently known as reducing sugars. Sucrose, on the other hand, is a non-reducing sugar, giving no precipitate with Fehling's solution, until it has been inverted by boiling or enzyme-action. It may be added that neither inulin nor the dextrins effect reduction of this reagent.

For microchemical purposes, especially when but small quantities of sugars are present, the following procedure is more advisable. The sections are mounted in a drop of a solution of phenylhydrazine hydrochloride in glycerine with which a drop of a solution of sodium acetate in glycerine (Appendix I) is thoroughly mixed. The preparation is heated for about an hour (although a longer period is often necessary) and allowed to cool. The phenylhydrazine reacts with many of the sugars to form insoluble yellow crystalline compounds, known as *osazones*. Glucose and fructose produce the same osazone, whose crystals appear as long needles arranged in sheaves (Fig. 45, A); that of maltose forms rosettes or plates of broad needles (Fig. 45, B), whilst in the case of cane-sugar no osazone is produced.

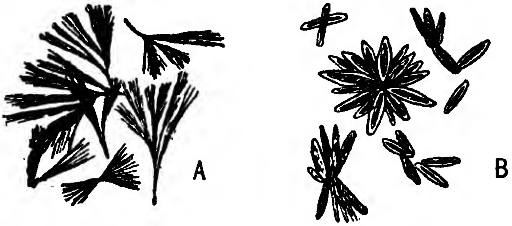

Fig. 45.—Osazones. A, of glucose; B, of maltose (after Plimmer).

Another method of storage of carbohydrate-material takes the form of strongly thickened cell-walls (cf. p. 84 and Fig. 39, A), as in many seeds (Date, Lupine, Coffee, etc.). Such walls consist of so-called *reserve-celluloses*, polysaccharides which differ somewhat from ordinary cellulose and break down more readily into simple sugars.

Of very common occurrence in plants are complex compounds known as *glucosides*, which, in the majority of cases, consist of glucose combined with one or more aromatic substances or other organic residue. On boiling with dilute mineral acids they split up into their constituents (hydrolysis). The decomposition of the glucoside within the plant is effected by special ferments which generally occur in distinct cells, so that the chemical process is not initiated until, for some reason (*e.g.* injury), ferment and glucoside come into contact. Thus, a glucoside amygdalin occurs in the seeds of the Bitter Almond (but not in the cultivated form), whilst the appropriate ferment *emulsin* is situated in the skin ; on crushing the seeds decomposition of the amygdalin into glucose, benzaldehyde, and prussic acid takes place, this last being responsible for the poisonous properties. The hot taste of many members of the Cruciferæ (*e.g.* Horse Radish, Cress) is due to the formation of mustard oil (together with glucose and potassium hydrogen sulphate) by the action of a ferment (*myrosin*) on another glucoside (sinigrin or myronate of potash).

In the two instances just given the glucosides undoubtedly render the plant distasteful to animals, but in many cases they seem to serve as a means of storing glucose in a form which does not diffuse readily. Thus the leaves of many Willows contain a glucoside salicin which, during the night, is split up by the enzyme *salicase* into glucose and saligenin ; the former is removed, whilst the latter combines with the new sugar formed the next day. To the glucosides also belong :—the saponins found in the Soapwort (*Saponaria*), *Quillaia*-bark, and many other plants, and easily recognised by the formation of a froth when shaken up with water ; the active principles of the Foxglove (*Digitalis*), the most important being digitalin, which has a profound effect on the action of the heart ; and the indican of the Woad (*Isatis tinctoria*) and of the Indigo-plant (*Indigofera*), the latter being the source of natural indigo.[1]

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[1] Vanillin, the cause of the aroma of Vanilla (obtained from the pod of *Vanilla planifolia*, a tropical Orchidaceous climber), is an aldehyde, similar to those often combined with glucose to form glucosides.

Oils or *fats* form another important group of reserve-substances found especially in those seeds in which carbohydrates are either scanty or absent (*e.g.* Castor Oil, Sunflower, etc.). Drops of oil are, however, not uncommon in the ordinary vegetative cells, and are particularly abundant in some lower plants [*e.g.* in some Algæ and in the Ergot of Rye (*Claviceps*)]. The vegetable fats are compounds (esters) of glycerine with various fatty acids (palmitic acid, oleic acid, etc.), and are decomposed by ferments (*lipases*, p. 183) into these two constituents. In most cases they occur as fluids within the plant, although the fat of the Cocoa (*Theobroma cacao*), the so-called Cocoa-butter, forms an exception to this.

The oil appears in the cell-sap or protoplasm as shining globular drops of varying size which are readily soluble in ether, benzene, etc.; some are even soluble in alcohol (*e.g.* those in the seeds of the Castor Oil). When a considerable quantity of fat is present (*e.g.* in the Brazil-nut), it can be squeezed out by pressure on to a piece of filter-paper, producing a greasy mark. The oil-globules turn pink or red on treatment with Scharlach Red (Appendix I), and assume a blackish colouration with osmic acid, which, however, also stains proteins and tannins in the same way. If sections of oil-containing material be placed in a solution of concentrated potash and ammonia in equal proportions, the globules after some time lose their sharply defined outline, and often become replaced by needle-shaped crystals. The change, spoken of as saponification, is due to the breaking up of the oil into glycerine and the fatty acid, the latter uniting with the alkali to form the corresponding salt.

Many plant-fats are of considerable economic importance; thus, olive oil is obtained from the fleshy fruit-wall of the Olive (*Olea europæa*, mainly cultivated in the Mediterranean region); coconut oil, used in the preparation of margarine, from the ripe seeds of the Coconut Palm (*Cocos nucifera*)[1]; and Castor Oil from the seeds of the Castor Oil plant (*Ricinus communis*). Other important commercial sources are Linseed (*Linum usitatissimum*), Cotton-seed (*Gossypium* spp.), Pea-nuts (*Arachis hypogæa*, with 38–50 per cent. of oil), and Soja-beans (*Glycine* spp.). In most cases the oil is extracted after crushing, the ultimate

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[1] Copra is the commercial name for the dried kernel of the Coconut.

residue forming so-called " oil-cake," which is extensively used for the feeding of cattle. Various vegetable oils are, moreover, employed in the manufacture of soap.

In the plant the fats are formed from carbohydrates and, since they contain a much smaller amount of oxygen, the volume of carbon dioxide evolved in breathing, during their formation, is considerably greater than that of the oxygen taken in. Conversely, when fats undergo change into carbohydrates during the germination of a seed, a large quantity of oxygen is absorbed in proportion to the carbon dioxide evolved. In correspondence with their low specific gravity, fats are a frequent form of non-nitrogenous food-reserve in seeds depending on wind-dispersal.

The carbohydrates or fats found in the various storage-organs are always accompanied by nitrogenous food-reserves, the most important and widespread of which are the *proteins*. We have already seen that very complex combinations of proteins are organised to form the living protoplasm, but simpler proteins often occur as non-living constituents of the ordinary vegetative cells, and are especially abundant in the diverse storage-organs. In the former case they may either be dissolved in the cell-sap or appear as crystal-like bodies, termed *crystalloids*, which may even be lodged in the plastids or nuclei. Succulent storage-organs, such as tubers, often likewise contain dissolved proteins, or these may take the form of crystalloids, as in the outer layers of a Potato ; but not uncommonly a considerable part of the nitrogenous matter in these cases is a mixture of simpler compounds known as *amides* (*e.g.* asparagin in the Potato and glutamin in the Beetroot).

In seeds proteins generally occur as small grains which are well seen in the cotyledons of a Pea or the endosperm of the Castor Oil. If a section of the former be treated with iodine, the minute protein granules take on a brown colouration, in sharp contrast to the blue or blackish starch-grains with which they are intermingled. On warming a section in a few drops of Millon's reagent (Appendix I), the whole assumes a brick-red colour which microscopic examination shows to be due to the proteins. Heating with concentrated nitric acid gives a yellow colouration which, on addition of ammonia, changes to orange (xanthoprotein reaction).

The proteins of oil-containing seeds (*e.g.* Castor Oil, Brazil-nut) occur in the form of especially large granules, known as *aleurone grains*. These appear to arise, as the seed dries during ripening, from the entire contents of vacuoles rich in protein-substance. Although the structure of aleurone grains is relatively complicated, they exhibit the characteristic protein-reactions mentioned above. If a thin section of the Castor Oil or Brazil-nut (from which the fat has been removed by soaking in alcohol and benzene respectively) be stained with iodine, the brown-coloured grains are readily seen under the microscope. Each shows a bounding membrane, the original membrane of the vacuole, enclosing amorphous protein in which two or more bodies are embedded. One of these, the crystalloid (Fig. 46, *Cr.*), is large and more or less angular, whilst the other, the globoid, is smaller and rounded (Fig. 46, *Gl.*); both consist of protein, but in the globoid, of which more than one may be present, this is combined with a double phosphate of calcium and magnesium. By mounting sections in water the amorphous ground-mass of the aleurone grain may be dissolved, and the bounding membrane rendered clearly visible; on the other hand, treatment

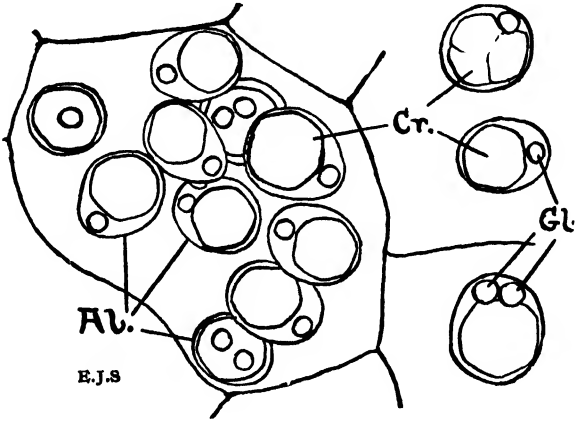

Fig. 46.—Aleurone grains (*Al.*) from the endosperm of the Castor Oil plant (*Ricinus*) showing the globoid (*Gl.*) and crystalloid (*Cr.*).

with dilute potash causes both bounding membrane and crystalloid to swell and disappear.

The protein-granules of the Pea, Bean, etc., are often regarded as small aleurone grains devoid of crystalloid and globoid. Similar structures occur in abundance in the so-called aleurone layer found at the periphery of the endosperm of Grasses (Wheat, Maize, etc.), just within the coat of the grain (Fig. 47). When the latter is detached, the protein-containing layer generally comes away with it, hence the greater nourishing properties of wholemeal bread as compared with that manufactured from white flour. For the same reason peeled potatoes are not so nutritious as those boiled in their skins, since the outer layers of the tuber contain protein-crystalloids (cf. above).

Proteins, owing to their complex molecules, are not readily diffusible, and consequently become converted into simpler, freely-diffusing compounds before they are transferred to parts where growth is occurring (*e.g.* in a germinating seed). This conversion is brought about by so-called *proteolytic enzymes* (*e.g.* pepsin, p. 183), which are in general similar to those occurring in the digestive tracts of animals, although some uncertainty exists as to the exact nature of those present in plants. The chief compounds produced, by the action of these enzymes on proteins, are firstly peptones and subsequently *amino-acids*. The former still exhibit the general characteristics of proteins, although they diffuse more easily, while the latter no longer possess protein-properties. Amino-acids are exceedingly common in growing and other parts of the plant (*e.g.* leucin in the buds of the Horse Chestnut, tyrosin in seedlings of the Lupine, etc.).

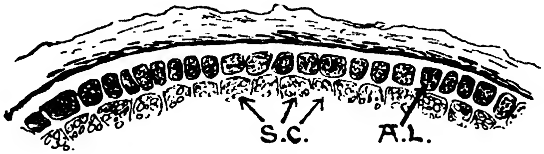

FIG. 47.—Aleurone layer (*A.L.*) of Wheat as seen in a transverse section. The starch-containing cells (*S.C.*) lie immediately beneath.

Approximate Food-content of Various Plant-products

(In percentages of the fresh weight)

	Starch.	Fats.	Proteins.[1]
Cocoa	4·2	50·4	13·3
Maize	68·4[2]	4·5	9·8
Oat	58·0[2]	5·2	10·4
Rice	75·0	0·5	9·0
Wheat	67·9[2]	1·8	12·3
Potato-tubers	20·0	0·15	1·9
Lettuce	2·2	0·3	1·4
Broad Bean	48·0[2]	1·6	23·0
Pea-nuts	5·2	44·0	30·0

The main classes of food-reserves (carbohydrates, fats, proteins) found in plants are thus the same as those constituting the diet of animals, but there is the difference already emphasised that the plant manufactures these from simple inorganic compounds, whilst the animal obtains them in the already elaborated form.

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[1] In most cases the percentages given are calculated for the entire nitrogenous organic matter.

[2] Total carbohydrates

CHAPTER X

BY-PRODUCTS AND SECRETORY ORGANS

THE by-products comprise chemical compounds formed during metabolism which do not, so far as our present knowledge goes, play any further part in the elaboration of food-substances. This does not, however, mean that they fulfil no functions in the living organism, for they may be of importance in warding off the attacks of preying animals, in the creation of attractive mechanisms, in the reduction of transpiration, etc.

One of the most widespread of the by-products is *oxalate of lime*, which may occur in practically every organ and tissue of the plant. It is produced by the neutralisation of the oxalic acid formed during metabolism, and, being insoluble, appears in the shape of crystals which assume diverse forms. Large *solitary crystals* (Fig. 48, C), each occupying the greater part of the cell-contents, are very common; but most frequent are clusters, or rosettes, of crystals radiating from a dark centre (Fig. 48, A). Another widespread type takes the form of bundles of needle-shaped crystals (*raphides*), generally situated in enlarged cells containing mucilage (Fig. 48, B). This last type is particularly characteristic of the Monocotyledons, though by no means lacking in Dicotyledons (*e.g.* Enchanter's Nightshade). In some cases, especially in the Potato-family (Solanaceæ), the oxalate of lime is deposited in the form of a powder-like mass of numerous very minute crystals (so-called *crystal-sand*).

Crystals of calcium oxalate are always found in quantity where active metabolism is going on. They are often very abundant in the tissues adjoining actively secreting organs (cf. p. 110); also in the leaves of deciduous plants, just prior to leaf-fall, features which respectively emphasise that this substance is a by-product, and that it is not generally useful to the organism.

The crystals of calcium oxalate are not soluble in acetic acid, but readily dissolve in sulphuric acid, with the production of calcium sulphate. The latter, being itself insoluble, becomes deposited promiscuously in the form of needle-like crystals. These tests serve to verify the presence of oxalate of lime, but in most cases their application is unnecessary, since crystals of other compounds are very rare.

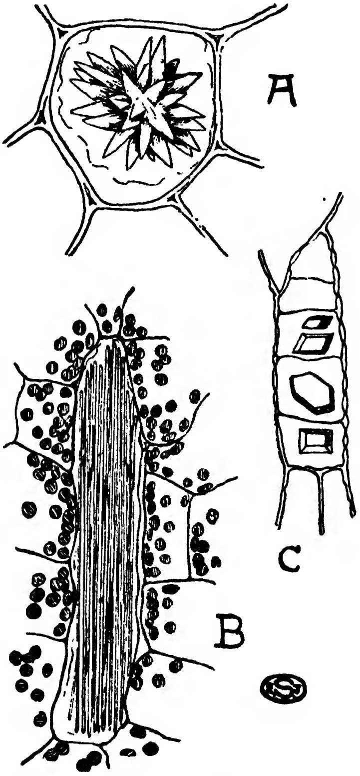

FIG. 48.—Crystals. A, Cluster crystals from leaf of Dog's Mercury (*Mercurialis*). B, Raphides from leaf of Enchanter's Nightshade (*Circæa*). C, Solitary crystals from phloem of Horse Chestnut (*Æsculus*).

Many by-products occur in solution in the cell-sap, and of these the commonest are diverse *organic acids* and bodies known as tannins. The former are responsible for the frequently acid reaction of the sap, and are especially abundant in unripe fruits. As examples mention may be made of malic acid (in Apples), citric acid (in Lemons), tartaric acid (in Grapes), etc.

The name of *tannins* is given to diverse organic substances, whose chemical constitution is not fully established, but all of which possess an astringent taste. Tannins are particularly common in the bark of trees (*e.g.* Oak, Alder), in unripe fruits (*e.g.* Pear, Acorn), in leaves (*e.g.* Bracken), and occur abundantly in certain abnormal growths (*e.g.* Oak-galls, cf. p. 204). The bark of certain trees (*e.g.* Oak), owing to the large quantity of tannin present, has long been employed in the conversion of hide into leather, which process depends on the coagulation, by the tannin, of the albuminous substances contained in the animal skin. The blue-black or greenish compounds of tannins with ferric salts have been extensively used in the preparation of ink.

Another group of by-products, encountered particularly in certain families of flowering plants (*e.g.* Ranunculaceæ, Scrophulariaceæ, Solanaceæ, Umbelliferæ), are the *alkaloids*. These are complex basic organic compounds containing nitrogen, which are either dissolved in the cell-sap or present in the solid state; in the plant they are often combined with organic acids. The alkaloids are of such importance, owing to their poisonous and medicinal properties, that the following list of some of the more familiar is given:

Alkaloid.	Action.	Source, etc.
Aconitine	Poisonous (used as an antipyretic).	Leaves, root, etc., of Monkshood (*Aconitum napellus*).
Atropine	Poisonous (various medicinal uses).	All organs of Deadly Nightshade or Belladonna (*Atropa belladonna*), seeds especially of Thornapple (*Datura stramonium*, Fig. 49) (Solanaceæ).
Cephaeline	Emetic (active principle of ipecacuanha).	Root of *Psychotria ipecacuanha* (Fam. Rubiaceæ, Brazil).
Cocaine	Local anæsthetic.	Leaves of *Erythroxylon coca* (Fam. Linaceæ, Bolivia and Peru).
Coniine	Poisonous (paralytic effect).	Seeds of Hemlock (*Conium maculatum*, Umbelliferæ).

Alkaloid.	Action.	Source, etc.
Hyoscyne	Poisonous (sedative).	Henbane (*Hyoscyamus niger*), *Atropa belladonna, Datura stramonium* (Fig. 49).
Morphine	Narcotic (active principle of opium).	Young fruits of Opium Poppy (*Papaver somniferum*).
Nicotine	Poisonous	Leaves of Tobacco (*Nicotiana tabacum,* Solanaceæ).
Quinine	Febrifuge	Bark of *Cinchona* spp. (Rubiaceæ).
Strychnine	Poisonous, heart and respiratory stimulant.	Seeds of *Strychnos nux-vomica* (Fam. Loganiaceæ).

The *ptomaines*, which are basic in character, are compounds produced during the decomposition of flesh, etc., by the agency of Moulds and Bacteria, but it is not altogether certain that the effects of so-called "ptomaine-poisoning" are solely due to these substances. Such stimulants as the caffeine of tea-leaves, coffee-beans, cocoa-beans, and Kola (*Cola acuminata*), and the theobromine present in the Cocoa, are derivatives of purine and very similar to the alkaloids.

The characteristic and often pleasing odour of such plants as Lavender, Mint, etc., and of many Umbelliferæ (*e.g.* Fennel), as well as of flowers, is due to the presence of so-called *volatile* or *ethereal oils*, which are composed of mixtures of hydrocarbons (*i.e.* compounds containing carbon and hydrogen only), known as terpenes, and of their oxygen derivatives. Examples are: peppermint oil, which contains the antiseptic menthol, from the Peppermint (*Mentha piperita*) ; oil of aniseed from the Aniseed (*Pimpinella anisum*); and the numerous oils from the many species of *Eucalyptus*. Similar oils are the essential principles of such spices as Cloves (the flower-buds of *Eugenia caryophyllata*), Cinnamon (the bark of young twigs of *Cinnamomum zeylanicum*), Ginger (the rhizome of *Zingiber officinale*), Pepper (the berries of *Piper nigrum*), etc.

Camphor is a solid terpene-derivative obtained from the wood of the Camphor-tree (*Cinnamomum camphora*), whilst turpentine is a mixture of terpenes which flows from the resin-passages (cf. p. 110) in the trunks of various species of Pines (especially *Pinus pinaster*) and of the Spruce Fir (*Picea excelsa*), when cuts are made in the surface of the trunk.

Most of the terpenes are colourless, highly refractive liquids, which evaporate completely if sections containing them are heated on a slide for about ten minutes. They are readily soluble in alcohol, chloral hydrate, glacial acetic acid, etc.

The colours of flowers are due in many cases to pigments, which are classed as *anthocyanins*, dissolved in the cell-sap of the petals, the colour being red, blue, or violet according to the acid or alkaline reaction of the sap. Such pigments are also frequently present in the vegetative organs, as, for instance, in the Beetroot and in the leaves of the Mother-of-Thousands (*Saxifraga sarmentosa*).

FIG. 49.—Photograph of part of the shoot, including two fruits, of the Thornapple (*Datura stramonium*), which contains the alkaloids atropine and hyoscyne. [Photo E. J. S.]

As mentioned above, it is doubtful whether any of these by-products are produced for their intrinsic utility to the plant. But it is quite possible that the poisonous alkaloids, the astringent tannins, or the pungent resins may render the plants containing them distasteful to herbivorous animals, and so prove indirectly beneficial. Similarly the antiseptic character of resin may well be of service in protecting a wound over which it has congealed. Tyndall showed that the vapour of ethereal oils tends to diminish the passage of heat through air, so that their common occurrence in plants of dry situations may be a means of checking evaporation by retarding the heating effect of sunshine. It may be, however, that some of the substances here referred to constitute a means of storage of food-material, and this applies especially to some of the tannins which seem to have the structure of glucosides.

Many of the by-products considered in this chapter collect as so-called *secretions* which are either deposited in glandular hairs (p. 134) on the surface or in special *secretory organs* within the body of the plant. Of the latter, the most striking are *secretory cavities, i.e.* large intercellular spaces (cf. p. 79), approximately isodiametric in form, and usually lodged in the parenchymatous tissues of the plant. In many cases they appear as transparent dots when leaves containing them are held up to the light, a phenomenon well seen in the St. John's Wort (*Hypericum perforatum*) and in the Rue (*Ruta graveolens*). In cross-sections of the leaves of the former the cavities appear more or less circular, each being lined with a layer of thin-walled, somewhat flattened cells (the *epithelium*, cf. Fig. 50, B, *S*), which discharge the secretion into the central space.

In the Rue, on the other hand, the cavities arise by a disorganisation of the secreting cells, whose remains persist at the periphery and no epithelial layer is present. Similar cavities are encountered in the heads of the Clove (Fig. 50, A) and in the skin of the Orange.

In the stems and roots of many plants (*e.g.* the resin-canals of Conifers) the secretions are contained in elongated *secretory canals.* In longitudinal sections these are seen to be extensive sinuous tubes which frequently branch and fuse, often pervading all the parenchymatous tissues of the plant. The difference between these canals and the secretory cavities is, however, only one of shape, not of kind.

It is a familiar fact that in some plants a milky, though sometimes coloured, juice (brilliant orange in the Greater Celandine, *Chelidonium majus*) issues from every cut or broken surface. This latex is especially found amongst British plants in members of the Poppy-family (Papaveraceæ), Spurge-family (Euphorbiaceæ), and in certain Compositæ, but it is still more characteristic of some tropical genera. The latex is contained in much-elongated tubes which constitute a branched system throughout the thin-walled tissues of the plant (Fig. 51).

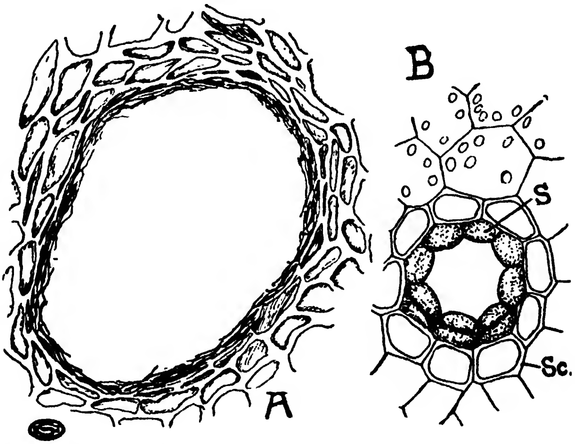

FIG. 50.—Secretory organs. A, Secretory cavity of the Clove (*Eugenia caryophyllata*). B, Secretory canal of the Ivy (*Hedera helix*) in transverse section. *S*, secretory epithelium ; *Sc.*, sclerenchyma sheath.

Latex, like milk, is an emulsion (cf. p. 70), the fluid basis of which is a solution of diverse substances (mineral salts, sugars, proteins, tannins, etc.). In some cases it includes an important active principle of the plant; for example, in the Opium Poppy (*Papaver somniferum*) the alkaloid morphine. The suspended particles include on the one hand oil-drops, on the other granules of resin, gum, protein, and caoutchouc. On exposure to air latex as a general rule congeals rapidly, a change often accompanied by discolouration; the "setting" is partly due to evaporation of water, but mainly to a confluence of the oil-globules and suspended particles. The coagulation of the latex, like that of blood, is of advantage in protecting and rapidly covering a wounded surface; moreover, the "dressing" in this case is even antiseptic. The laticiferous elements further serve as food-reservoirs, and may have a rôle in the transport of food-material.

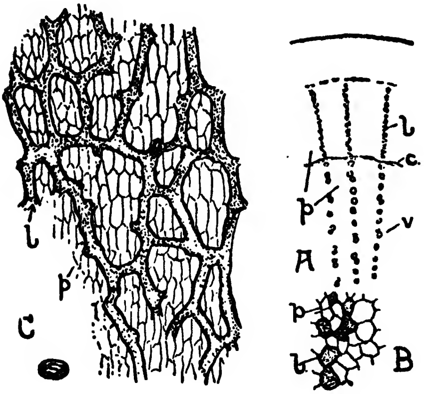

Fig. 51.—Laticiferous tubes in the root of the Salsify (*Tragopogon*). A, Diagrammatic representation of a small part of a transverse section, showing the distribution of the laticiferous tubes (*l.*), in relation to the cambium (*c.*), and the vessels of the xylem (*V.*). B, a small part of the secondary phloem enlarged. C, Longitudinal section. *p.*, parenchyma.

Those plants, whose latex contains a considerable percentage of caoutchouc-particles, are of great economic importance, since they are the source of the *rubber* and *gutta-percha* of commerce (*e.g.* Para-rubber from *Hevea brasiliensis* and Ceara-rubber from *Manihot glaziovii*).

CHAPTER XI

THE STRUCTURE OF ROOTS

IN the mature plant the different types of elements are grouped together to form *tissues* subserving diverse functions. Thus, for instance, one tissue, which is always superficial and has the general function of protecting the underlying parts, constitutes the epidermis. The vascular tissues, comprising the wood or xylem and the bast or phloem, form the principal conducting systems for water and mineral salts, and for elaborated food-substances, whilst others—largely parenchymatous in character—go to form the general matrix or ground tissue. It must not be supposed, however, that, because there is one general function, the component elements of these and other tissues are necessarily uniform in character, a fact that will be best realised by the study of concrete examples.

In the young root we have distinguished a number of regions, beginning with the *root-cap*, covering the growing point (Figs. 15, *r.c.*, and 34), and followed successively by the zone of elongation, the zone bearing root-hairs, and the older part where the root-hairs have usually withered and lateral roots (Fig. 18, *l.r.*) are emerging through the surface-layers, commonly in four or five vertical rows. In a longitudinal section through the tip of the root the cap is found to consist of a number of concentric layers of thin-walled parenchymatous cells, whose arrangement becomes less regular towards the outside (Fig. 34). The outermost cells gradually become mucilaginous and break down, whilst the substance of the cap is constantly renewed from the underlying meristem. A little way behind the growing point (p. 73) the middle of the root is occupied by a continuous, rather denser strand of elongated elements, which develop into the vascular tissue, and which offer a marked contrast to the thin-walled parenchymatous cortex around (cf. Fig. 2, A and B).

The general structure of the root can best be studied in a cross-section through the mature region, the Creeping Buttercup (*Ranunculus repens*) furnishing suitable material for a first example. Under the low power of the microscope the broad parenchymatous *cortex* (Fig. 52, *C.*), whose cells contain numerous starch-grains (*s.*), and the central conducting strand, are again sharply contrasted. At the edge of the section is a layer of shrunken cells (Fig. 53, *r.*), some of which are prolonged into shrivelled root-hairs. This epidermis withers above the zone of root-hairs and, since its chief function is their production, it is more usually termed the *piliferous layer*. It is only in sections cut nearer the growing tip that its cells are as yet uncontracted, and can be seen to form a single layer.

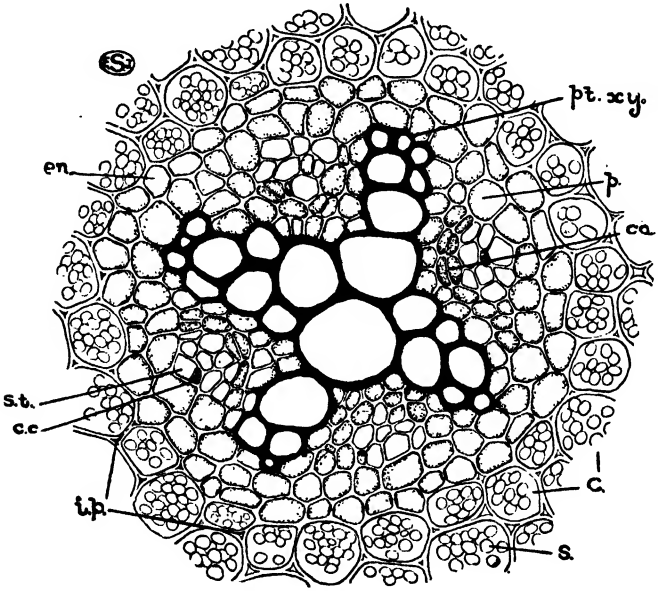

FIG. 52.—Transverse section of the central part of the root of the Creeping Buttercup (*Ranunculus repens*). The walls of the xylem elements are shown black. *C.*, inner part of cortex ; *ca.*, cambium ; *c.c.*, companion cell ; *en.*, endodermis ; *i.p.*, intercellular spaces ; *p.*, pericycle ; *pt.xy.*, protoxylem ; *s.*, starch ; *s.t.*, sieve-tube.

The *root-hairs*, each arising from a separate cell (Fig. 17, *r.h.*), appear as tubular unbranched outgrowths with bluntly rounded tips. The greater part of any root-hair is occupied by a large vacuole continuous with that of the epidermal cell and filled with sap. There is consequently only a thin lining layer of cytoplasm, which is best seen near the tip where the single nucleus usually lies embedded (Fig. 74).

Beneath the withered piliferous layer, in the older part of the root, lies the *exodermis* (Fig. 53, *Ex.*), a layer of protective cells which are on the whole rather smaller than the adjacent cells of the cortex. Their brownish, slightly thickened walls are chemically changed (*i.e.* suberised, cf. p. 151) in such a way that they are almost impermeable to water; but this alteration does not usually take place till the root-hairs begin to wither, so that the water they absorb can readily pass inwards to the vascular cylinder. In some cases, however (*e.g.* in most Monocotyledons), where the exodermis differentiates at an early stage, thin-walled passage-cells, through which the water travels, are found at regular intervals.

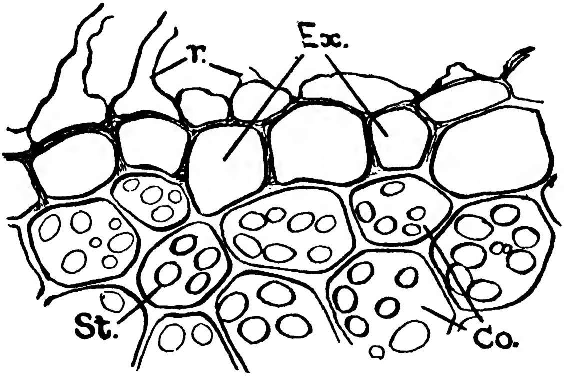

FIG. 53.—Piliferous layer (in part withered) and exodermis of the root of the Creeping Buttercup (*Ranunculus repens*). *Co.*, cortex; *Ex.*, exodermis; *r.*, root-hairs arising from cells of piliferous layer; *St.*, starch.

The cell-walls of the *cortex* become thinner towards the centre, and intercellular spaces (Fig. 52, *i.p.*) are abundant. The latter form a continuous system which permits of gaseous exchange with the aerial parts of the plant. The vascular strand is de-limited from the cortex by two well-defined layers of cells, an outer, the endodermis (*en.*), and an inner, the pericycle (*p.*) (cf. below).

In sections stained with aniline chloride a four-rayed group of yellow elements, composing the lignified wood or *xylem* (Fig. 52), is seen to occupy the greater part of the conducting strand. In the bays between the four arms of the xylem are oval groups of small-celled unstained tissue, the *phloem*, in which the wide and empty-looking sieve-tubes (*s.t.*) are plainly distinguished from the narrower companion-cells (*c.c.*) with their dense contents (cf. p. 82). Each phloem-group is separated from the adjacent xylem by one or two layers of parenchyma (*ca.*).

The xylem consists chiefly of dead, empty-looking elements, the vessels, of which those at the centre of the conducting strand are the largest, whilst the remainder become progressively smaller in passing outwards along any one of the rays. The end of each xylem-arm, immediately beneath the pericycle, is thus occupied by a strand of the narrowest vessels (Fig. 52, *pt.xy.*). In cross-sections, through younger parts of the root, a larger or smaller number of the central vessels will appear thin-walled and unlignified, showing that differentiation of the xylem takes place from without inwards. The small peripheral elements are consequently spoken of as *protoxylem*, and the larger, later-formed ones as *metaxylem*.

Longitudinal sections passing through one of the xylem-arms will show that the vessels of the protoxylem are spirally thickened, whilst those of the metaxylem bear bordered pits. The walls between the larger vessels, in the transverse section, exhibit a thin dark line down the middle (the middle lamella), with the thickening layers on either side. These latter are not homogeneous, however, but appear to consist of short dark lengths alternating with lighter and narrower portions, where the pits are seen in optical section.

The cells of the *endodermis* (Fig. 52, *en.*) are distinctly smaller than the adjacent cortical cells and somewhat flattened. Their radial walls are thicker and look darker than the others, although when sharply focussed in optical section they appear bright owing to their highly refractive character. On treatment of a section with strong sulphuric acid, the membrane swells and dissolves, except for the radial walls, which persist unaltered, implying that they are chemically different from the other walls of the endodermal cells. These features of the radial walls are commonly exhibited by the endodermis of roots.

The *pericycle* which lies immediately within the endodermis is another continuous layer not characterised by any structural peculiarities (Fig. 52, *p.*).

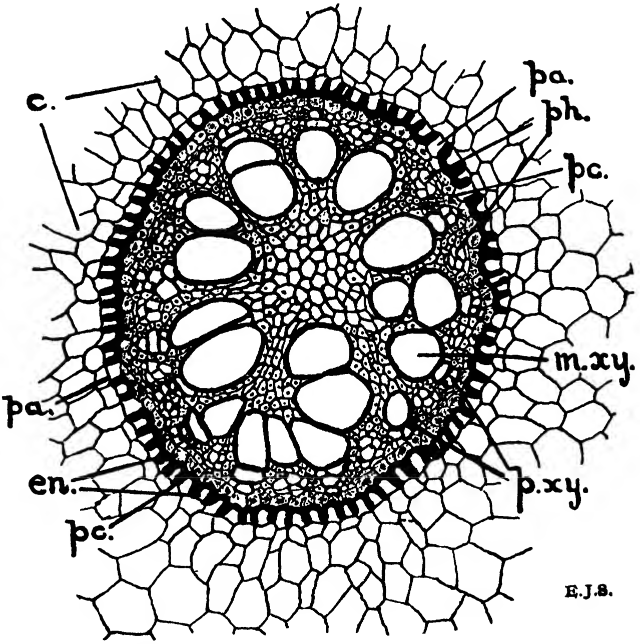

FIG. 54.—Transverse section of the central part of the root of the *Iris*. *C.*, cortex ; *en.*, thick-walled endodermis ; *m.xy.* metaxylem ; *pa.*, thin-walled passage cell in endodermis ; *p.c.*, pericycle ; *ph.*, phloem ; *p.xy.*, protoxylem.

Many of the features just described are typical of roots generally, viz. the aggregation of the vascular tissue near the centre ; the alternation of phloem and xylem resulting in a radial structure ; the peripheral location of the protoxylem ; the wide cortex ; the differentiation of the endodermis ; and the occurrence of exodermis and piliferous layer. Roots differ among one another in two principal respects—namely, as to the number of phloem- and xylem-strands, and in the presence or absence of parenchyma (pith) in the centre of the conducting tissue. As regards the former feature, there may be two or more of such strands, roots being described as *diarch*, *triarch*, *tetrarch* (Fig. 52), *pentarch*, etc., according as the number of alternating xylem- and phloem-groups is two, three, four, or five, etc., whilst when they are numerous the structure is said to be *polyarch* (Fig. 54). Thus the root just examined is tetrarch, that of the Wallflower diarch, and that of most Monocotyledons polyarch. A *pith* composed of parenchyma, which is sometimes thick-walled, is frequent in the roots of herbaceous Dicotyledons and in Monocotyledons (Fig. 54). Roots also vary in the manner of thickening of the mature cells of the endodermis (cf. Fig. 54, *en.*).

The root of the *Iris* (Fig. 54) illustrates the typical Monocotyledonous structure, viz. a central pith and numerous alternating groups of xylem and phloem.

It is evident that the structure of the root is well suited to its functions of water-absorption and anchorage. The out-growth of the cells of the piliferous layer into root-hairs affords an enormously increased surface through which absorption can take place. The more or less extensive branching of the root and the central location of the mechanical tissues (*i.e.* xylem and thick-walled pith) enables it to withstand the pulling strains to which it is subjected when the shoot sways to and fro in the wind.

Many plants characteristic of soils rich in humus exhibit an intimate relation of fungal threads (*mycorrhiza*) with their roots or other underground organs. The advantage of this association would appear to depend mainly on the power of the Fungi to break down and absorb the organic material which is then in part utilised by the flowering plant (cf. p. 243).

CHAPTER XII

The Structure of the Young Stem

The comparatively slight variation in the anatomical construction of roots can be related to their very uniform environment (the soil) ; in fact, the only marked departures from the normal are associated with the fulfilment by the roots of special functions. Stems, on the other hand, develop under very diverse conditions as regards mechanical strains, illumination, supply of moisture, etc., and consequently display much more varied structure. Moreover, the general plan of construction of the stem differs from that of the root in several important respects.

The organisation of a Dicotyledonous stem can be studied in a cross-section through the uppermost internode of a young Sunflower (Fig. 55). The most obvious feature is that the vascular tissue is a ring broken up into distinct *vascular bundles*. In each the thick-walled xylem (*xy.*) is towards the inside and the thin-walled phloem (*ph.*) towards the outside, the two thus lying on the same radius (constituting a *collateral* bundle), in contrast to the alternate arrangement of these tissues obtaining in the root. By the disposition of the vascular bundles in a ring the ground tissue is marked out into three regions, namely the *cortex* (Fig. 55, *c.*) on the outside, the *pith* (*p.*) in the centre, and the *rays* (often called medullary rays, *r.*) connecting the two and separating adjacent bundles. The terms *pith*, *cortex*, and *rays* are, however, purely topographical, and do not necessarily imply any differentiation between the component cells, which in fact, in most cases, are largely thin-walled and parenchymatous in all three regions (cf. Figs. 55 and 56). The edge of the section is bounded by an *epidermis*[1] which differs

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[1] For a detailed consideration of epidermis and stomata, see the next chapter.

from that of the root in having strongly thickened outer walls. It forms a continuous layer except where interrupted by the presence of stomata[1] or lenticels (p. 45). Its function is to protect the more delicate internal tissues, and in correspondence with this it does not wither at an early stage like the piliferous layer. Occasional cells grow out into hairs (Fig. 55, *h.*), but these are quite different in character from the root-hairs.

Immediately within the epidermis are several layers of collenchymatous cells (Fig. 55, *s.*), thickened mainly on the tangential walls, whilst between the cells of the inner layers are relatively large intercellular spaces. Such spaces are also abundant in the remainder of the ground tissue, and form small triangular cavities between the polygonal cells of the pith.

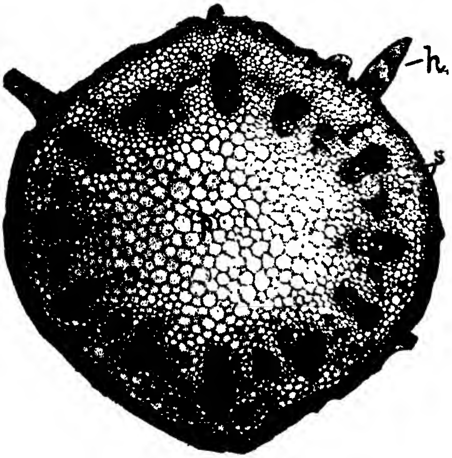

Fig. 55.—Photomicrograph of a transverse section of the young stem of the Sunflower (*Helianthus*). *c.*, cortex ; *h.*, hair ; *p.*, pith ; *ph.*, phloem ; *r*, rays ; *s*, collenchyma ; *xy.*, xylem.

At the inner limit of the cortex there is a single layer of cells distinguished by the frequent presence of large starch-grains, which can be rendered still more prominent by staining with iodine. The layer in question bends outwards around each

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[1] For a detailed consideration of epidermis and stomata, see the next chapter.

vascular bundle, and so presents a sinuous outline. Such a *starch-sheath* is not uncommon in herbaceous Dicotyledonous stems (cf. Fig. 68, *S.s.*).

The zone of tissue between the starch-sheath and the phloem constitutes the *pericycle*, which, in the Sunflower, is composed of groups of fibres (as yet not fully thickened) opposite the bundles (Fig. 56, *f.*; Fig. 68, F), and elsewhere of parenchyma (Fig. 55). In other plants the pericycle is often parenchymatous throughout, consisting of one or more layers of cells.

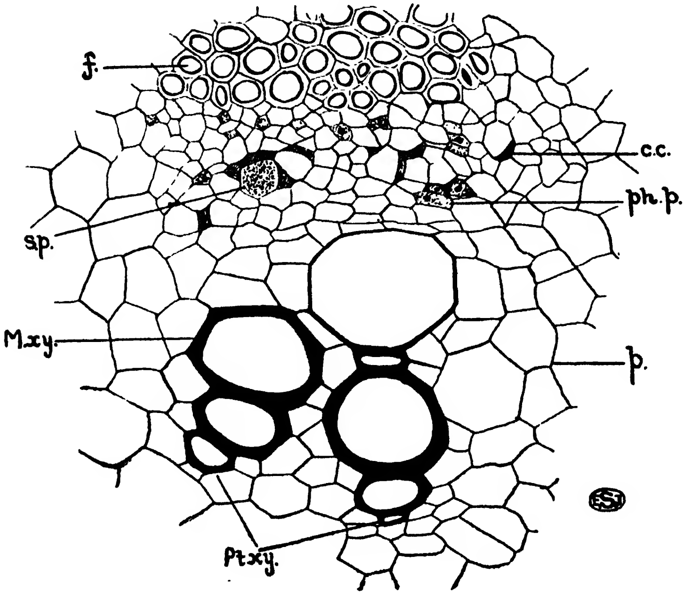

Fig. 56.—A single vascular bundle from the stem of the Sunflower (*Helianthus*) in transverse section. *c.c.*, companion cells (shaded); *f.*, fibres of the pericycle; *M.xy.*, metaxylem; *p.*, parenchyma of the rays; *ph.p.*, phloem-parenchyma; *Pt.xy.*, protoxylem; *s.p.*, sieve-plate.

In the individual bundles the phloem can be distinguished by the shining appearance of the cell-walls, as well as by the unequal size of its component elements (Fig. 56). The large, empty-looking sieve-tubes, exhibiting an occasional sieve-plate (*s.p.*) and associated with small companion cells (*c.c.*), which have dense contents, are intermingled with ordinary parenchyma-cells (*phloem-parenchyma*, *ph.p.*). Two or three layers of flattened thin-walled cells, situated between the phloem and the xylem, constitute the *cambium* (cf. Fig. 68, C, p. 142), a meristematic region which becomes active in the older stem and forms additional vascular tissue (cf. Chapter XV).

The wood consists of radial files of vessels separated by rows of smaller parenchymatous cells (the *wood-parenchyma*, Fig. 56). The smallest vessels (*Pt.xy.*), which represent the *protoxylem* (cf. p. 116), are situated nearest the pith, while the larger metaxylem-elements (*M.xy.*) are towards the outside, a further point of contrast to the root. In a longitudinal section the spiral thickening of the protoxylem and the pitted elements of

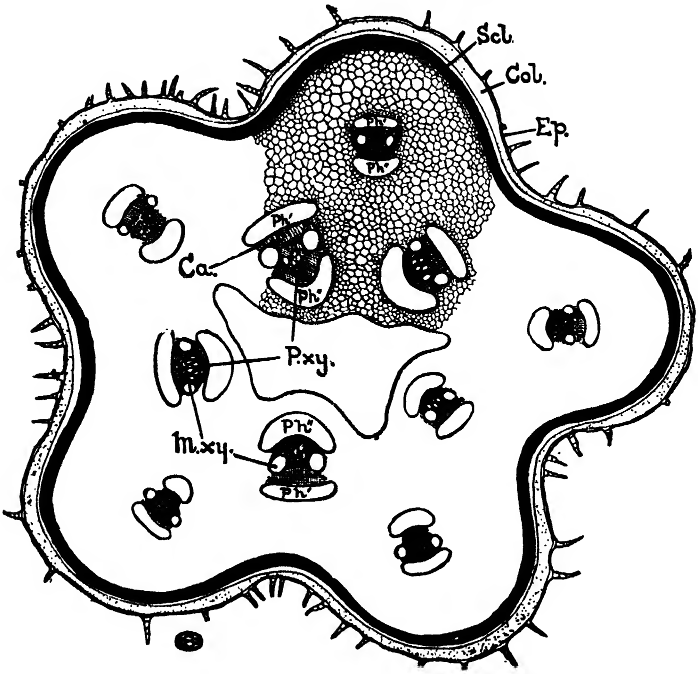

FIG. 57.—Diagram of a transverse section of the stem of the Vegetable Marrow (*Cucurbita*). *Ca.*, cambium ; *Col.*, collenchyma ; *Ep.*, epidermis ; *M.xy.*, metaxylem ; *Ph.'*, outer phloem ; *Ph.''*, inner phloem ; *P.xy.*, protoxylem ; *Scl.*, sclerenchyma (black).

the metaxylem can be recognised. The wood-parenchyma cells have more or less thickened walls, which are lignified like those of the vessels, but they nevertheless retain their living contents. Small cells resembling the wood-parenchyma, but not lignified, form a sheath (the *medullary sheath*, Fig. 55) at the inner edge of each bundle.

Further insight into the structure of the Dicotyledonous stem will be afforded by a study of that of the Vegetable Marrow (*Cucurbita*) (Fig. 57). The transverse section differs from that of the Sunflower in the hollow pith, in the presence of a broad ring of sclerenchyma (*Scl.*) some little way beneath the epidermis, and in the arrangement and construction of the vascular bundles.

There are here two rings of bundles, of which the larger and inner alternate with the smaller and outer (Fig. 57). Two groups of phloem occur in each bundle, one external (*Ph.'*), separated from the xylem by the cambium (*Ca.*), the other internal (*Ph.''*), separated from the protoxylem (*P.xy.*) by ordinary parenchyma. Such bundles, termed *bicollateral*, are not uncommon in certain families of Flowering Plants, such as the Potato-family or Solanaceæ, and offer a marked contrast to the normal collateral type seen in the Sunflower. The elements of both xylem and phloem are remarkably large, and are therefore especially suited for a study of their detailed structure, which can be rendered more distinct by staining with eosin (see Appendix V).

In the *phloem* many of the large somewhat thick-walled sieve-tubes appear empty; but here and there, where the plane of section coincides with a separating wall, there is a deeply stained sieve-plate (Fig. 38, *s.p.*), recognisable by its dotted structure. Under the high power the sieve-plate exhibits an irregular network of thickening, completely covered by a thin layer of cytoplasm, the greater part of each mesh being occupied by an open pore through which communication with the next segment of the sieve-tube is established. In contact with each sieve-tube are one or more small, often more or less triangular companion cells (Fig. 38, *c.c.*), with dense contents. The numerous phloem-parenchyma cells (Fig. 38, *p.*) are more or less intermediate in size, but without either the thickened wall of the sieve-tube or the dense contents of the companion cell. Both inner and outer phloem show the same structure.

In longitudinal sections (Figs. 38, left, and 58) the horizontal sieve-plates (*s.p.*), stained red with the eosin, occur at frequent intervals in the course of the sieve-tubes. When viewed in optical section, they present an interrupted appearance, due to the alternation between the pores and the bars of thickening with their covering of cytoplasm. Thick, highly refractive masses (stained red by the eosin), composed of a carbohydrate known as *callose*, are often found on one or both sides of the sieve-plates. Callose is distinguished by being insoluble in ammoniated copper oxide, but soluble in a 1 per cent. solution of caustic potash.

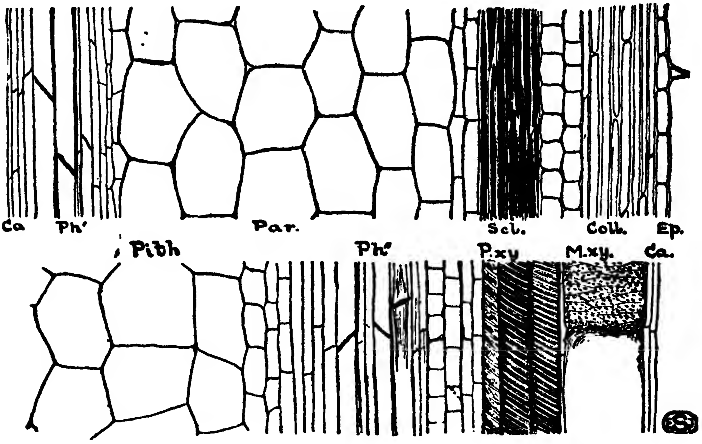

FIG. 58.—Longitudinal section through the stem of the Vegetable Marrow (*Cucurbita*). *Ca.*, cambium; *Coll.*, collenchyma; *Ep.*, epidermis; *M.xy.*, metaxylem; *Par.*, parenchymatous cortex; *Ph.'* and *Ph."*, outer and inner phloem; *P.xy.*, protoxylem; *Scl.*, sclerenchyma.

Here and there the plane of the section passes through a companion cell (Fig. 38, *c.c.*) in contact with its sieve-tube. The former tapers off towards the sieve-plates above and below, so that its length coincides with that of the sieve-tube segment from which it was cut off. The large nucleus can generally be seen embedded in the dense cytoplasm which completely fills the cell. The phloem-parenchyma cells (Fig. 38, *p.*) are readily distinguished by their shape from the other elements. The cells of the cambium (Fig. 58, *Ca.*) appear much elongated in the longitudinal section and have chisel-shaped ends.

In the transverse section of the *wood* one can recognise, as in the Sunflower, small protoxylem-elements towards the interior (Fig. 57, *P.xy.*), large metaxylem-vessels beyond (*M.xy.*), and numerous intermingled wood-parenchyma cells. Where two vessels are in contact, the middle lamella between the pitted thickening layers of the common wall can be clearly made out. In longitudinal sections the broad metaxylem-vessels (Fig. 58, *M.xy.*) show reticulate thickenings which are in marked contrast to the spiral thickenings of the protoxylem-vessels (*P.xy.*); the slight constrictions occurring at short intervals mark the limits of the cells from which the vessel was built up, and, in thick sections, the ring-like remnants of the original septa can often be distinguished. The exceptionally large vessels are a marked feature of many other climbers besides the Vegetable Marrow.

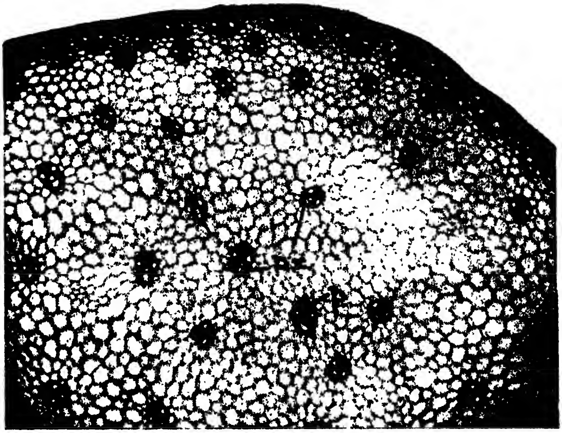

FIG. 59.—Photomicrograph of part of a transverse section of the stem of the Maize (*Zea mais*). *p.*, phloem; *p.x.*, protoxylem.

Stems of Monocotyledons (of which the Maize furnishes a typical instance) usually exhibit a large number of bundles which frequently appear scattered throughout the whole of the ground tissue (Fig. 59), so that a definite cortex and pith cannot be distinguished. The bundles, though differing in certain details, show the same general structure, being collateral with xylem and phloem on the same radius and with the protoxylems (*p.x.*) directed inwards. There is no cambium between the xylem and the phloem, an important respect in which the Monocotyledonous bundle usually differs from that of the Dicotyledon. The phloem tends to be sunk between the two large metaxylem vessels, and, owing to rapid elongation of the stem, the protoxylem vessels undergo early rupture and give rise to an irregular cavity (cf. p. 89). The bundles are commonly enveloped in a sheath of small, thick-walled cells (often fibres), a feature also encountered in some Dicotyledons (*e.g.* Buttercup).

The functions of the stem are manifold, but among the most important are those of bearing leaves and flowers, and of constituting a connecting-link between the root-system and the foliage. The shoot of the ordinary erect plant is most liable to bending, under the influence of the wind, etc., and thus contrasts with the root, which is exposed chiefly to pulling strains. Related to this the *mechanical elements* of the stem are more or less symmetrically arranged near the periphery. In the young stem the upright position is maintained by the frequent subepidermal collenchyma (Figs. 40, 55, and 57), by the xylem of the bundles, and by the turgidity of the living cells (cf. also p. 155). As the stem matures, additional mechanical tissue is often furnished by the development of pericyclic fibres (*e.g.* Sunflower, Fig. 56, *f.*), of a thick-walled sheath to the bundles (Monocotyledons, Buttercup), or of a zone of sclerenchyma in the cortex (*e.g.* Vegetable Marrow, Fig. 57, *Scl.*).

Most young stems exhibit *chloroplasts* in the cortical cells, the carbon dioxide requisite for photosynthesis being obtained from the intercellular spaces between them, which communicate with the atmosphere by means of occasional stomata (cf. p. 129) in the epidermis.

Whilst it has been seen that the arrangement of the tissues differs materially in root and stem, all the tissues in the two organs pass over imperceptibly into one another.

CHAPTER XIII

THE EPIDERMIS

THE surface of the shoot is protected by a skin, or *epidermis*, composed of one layer of living cells which possess certain marked characteristics. In transverse sections the cells usually appear somewhat flattened with slightly convex outer walls, whilst the lateral and inner ones are generally straight ; moreover, they fit closely together without intercellular spaces (Fig. 65, *Ep.*). The epidermal cells have living contents, usually contain plastids, and possess large vacuoles filled with watery, generally colourless, sap. Chloroplasts are not developed in the cells in well-illuminated situations, but are often present in the epidermis of submerged aquatics or of land-plants when growing in the shade.

The outer epidermal walls in most cases are more strongly thickened than the others, and so changed (*cuticularised*) as to render them more or less impermeable to water vapour and gases. The exact nature of the modification is not known, but it appears to consist essentially in impregnation with substances of a fatty or waxy character; these are most abundant in the outermost region of the external walls, which forms a continuous, relatively impermeable, layer over the whole epidermis (except for the stomata) known as the *cuticle* (Fig. 61, *Cu.*). The latter is insoluble in cuprammonia and concentrated sulphuric acid, being the only part of the epidermis that does not dissolve in this reagent. The cuticle is easily stained with Scharlach Red, probably as a result of the presence of fatty substances.

Owing to its toughness, the cuticle, especially when strongly developed, renders the epidermis more efficient as a protection against mechanical injury; but its main function is certainly the restriction of transpiration to the stomata (cf. p. 158). In correspondence with this its thickness depends mainly on the nature of the habitat; thus the cuticle is most strongly developed in plants of dry situations (*e.g.* Gorse), whilst it is extremely thin in submerged aquatics, where absorption of water takes place over the whole surface. Most young organs, before they have attained their full size, possess but a very thin cuticle through which considerable transpiration takes place; hence the necessity for other devices for the reduction of transpiration (*e.g.* hairs, folding of leaves, etc.). Even a very thick cuticle is, however, not completely impermeable.

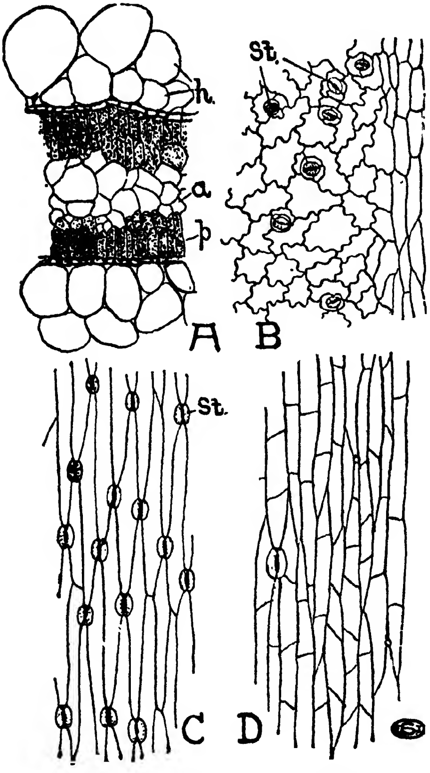

FIG. 60.—Structure of the epidermis. A, Transverse section of leaf of Silver Goosefoot (*Obione portulacoides*) showing the bladder-like hairs (*h.*), the water-holding tissue (*a.*), and the palisade layer (*p.*) B, Surface section of leaf of Ground Ivy (*Nepeta glechoma*). C, Surface section of leaf of Onion. D, Surface section of stem of Runner Bean (*Phaseolus multiflorus*). *St.*, stomata.

Not uncommonly the epidermis can be readily stripped off and so examined in *surface view*, when it will again be seen to form a continuous layer (Fig. 60, B–D) without intercellular spaces, the only gaps being constituted by the stomata to be described below. The shape of the cells in such surface sections is very varied. In stems (Fig. 60, D) and in the leaves of most Monocotyledons (Fig. 60, C) they are usually considerably elongated parallel to the longitudinal axis, whilst in Dicotyledonous leaves they are in most cases roughly isodiametric (Fig. 60, B). Where the lamina is thin the lateral walls of the epidermal cells are often undulated (Fig. 60, B). Through this wavy outline the cells interlock, so that the surface of contact between them is increased, and the risk of tearing by the wind is proportionally diminished.

In plants of dry habitats the epidermal cells may attain a considerable size and serve for the storage of water, which is possibly always a function of this layer. In extreme cases water may be stored in localised enlargements, which often project as water-containing *hairs* or bladders (*e.g.* the Ice-plant, *Mesembryanthemum crystallinum*, and the Silver Goosefoot, *Obione portulacoides*, Fig. 60, A, *h*.)

The pronounced thickening and cuticularisation of the outer walls of the epidermal cells, and the absence of intercellular spaces between them, endues the epidermis as a whole with considerable strength. It hence serves both as a mechanical protection and also as a light-screen for the underlying chlorophyll.

Most important of all, it checks evaporation from the general surface of the plant, and indeed, where the cuticle is thick, transpiration is almost entirely restricted to the special apertures or stomata considered in the next paragraph. Beneath the upper epidermis a second layer of colourless cells (*hypoderm*), which are usually thick-walled, is sometimes present.

The general characteristics of *stomata* are readily studied by stripping off a piece of the epidermis from a fresh leaf of the *Iris*. Scattered among the colourless elongated cells are oval stomata, each consisting of two bean-shaped *guard-cells* (Fig. 61, A, *g.c.*; see also Fig. 60, C) surrounding the narrow elliptical *pore* by means of which the intercellular spaces of the leaf communicate with the atmosphere. The guard-cells contrast with the ordinary epidermal cells in containing numerous chloroplasts and starch-grains, and are especially distinguished by the uneven thickening of their walls, which are thin on the side away from the pore, but markedly thickened around the latter (Fig. 61, A, B). Each guard-cell has a well-developed protoplast and a prominent nucleus. The ordinary epidermal cells almost meet above the guard-cells, so that the latter are only plainly visible on focussing to a lower level (Fig. 61, A, B); in this way the pore comes to be situated at the bottom of a miniature hollow constituted by the surrounding cells, and the stoma consequently occupies a sheltered position. This feature is especially marked in plants of dry situations, but in those growing in damp, shady habitats the guard-cells are often level with or raised above the adjacent epidermis.

The overarching of the guard-cells by the adjoining epidermal cells is equally obvious in a transverse section (Fig. 61, B) of the *Iris*-leaf. Here each guard-cell appears approximately oval

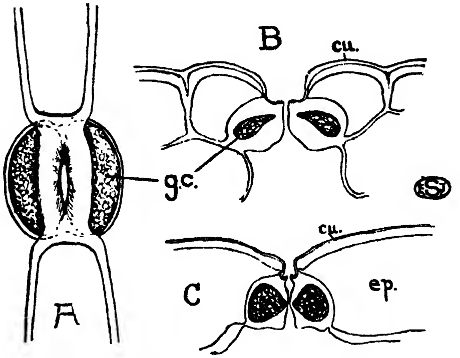

Fig. 61.—Structure of stomata. A, in surface view; B and C, in transverse section. A, B, *Iris germanica*. C, Onion (*Allium cepa*). *cu.*, cuticle; *ep.*, epidermal cell; *g.c.*, guard-cells.

in form and provided with thick walls, the thickening being especially marked adjacent to the pore, and giving rise to a slight upwardly projecting ridge at the outer edge of the aperture. In many plants, however, the walls of the guard-cells are not so uniformly thickened, those remote from the pore being relatively thin, whilst those towards the aperture show a marked decrease in thickness opposite the middle of the pore (*e.g.* Onion, Fig. 61 C). As a result of this unequal distribution of the thickening, the cavities of the guard-cells taper abruptly in the direction of the pore, so that a maximum thickness is obtained towards the upper and lower sides (Fig. 61, C). Beneath the stoma lies an air-space, the *respiratory cavity* (Fig. 65, *R.*), serving for the immediate interchange of gases and water-vapour between the intercellular system of the plant and the air around.

The vertical leaf of the *Iris*, in which both surfaces are alike, bears almost the same number of stomata on each. Moreover, the latter are all placed parallel to the axis, as is usual for the elongated leaves of Monocotyledons (Fig. 60, C) and the epidermis of young stems; in the latter case, however, the stomata are often few in number. Those of horizontal dorsiventral leaves (*e.g.* of most Dicotyledons) are chiefly situated on the lower surface, being sometimes altogether absent from the upper (*e.g.* most trees), and, moreover, exhibit an irregular arrangement (Fig. 60, B). The restriction of the stomata to the lower surface in such leaves obviates the risk of their being blocked by particles of dust or moisture and protects them from the direct heating effect of the sun.

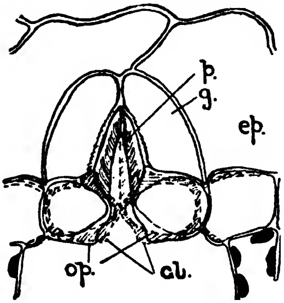

FIG. 62.—Half of a stoma, seen in perspective, showing the positions of the guard-cells in the open (*op.*, firm lines) and closed (*cl.*, dotted lines) conditions. *ep.*, epidermis; *g.*, guard-cell; *p.*, pore.

On mounting a strip of the fresh epidermis of some leaf in water, the open pores of the stomata are readily visible, being usually occupied by air. On transference to glycerine or a 5 per cent. sugar solution, which will reduce the turgor of the guard-cells, the width of the pores decreases appreciably (*i.e.* they " close "), but when returned to water the turgor is restored and they again open. Measurement shows that, though there is usually no marked change in length, there is an appreciable increase in width, when the stoma opens (cf. Fig. 62). The alteration in form of the guard-cells, to which the variation in the size of the stomatal aperture is due, is thus primarily determined by changes in turgescence.

The *mechanism* is, however, directly dependent on the unequal distribution of thickening which, in transverse section, has been seen to be mainly localised around the upper and lower edges of the pore; on the other hand, the middle of the convex wall next to the pore, as well as the curved wall remote from the pore, remain comparatively thin (Fig. 61, C). When the guard-cells are turgid and the thin walls stretch, the pull exerted separates the thick walls, thus opening the pore (Fig. 62, *op.*). As seen in section, opening of the stoma is accompanied by a flattening of the convex walls on each side of the pore and an increased convexity of the unthickened walls. As a result there is movement of the guard-cells at the lines of junction with the adjacent epidermis both above and below, due to the bulging of the walls away from the pore (cf. also p. 158).

A rough model of a stoma may be made in the following way: A straight piece of the flower-bearing stalk of a Jonquil or the internode of a Dog's-mercury, about 3 to 4 inches long, is halved lengthwise, the two halves being then placed in a strong solution of salt until they become flaccid. They are thereupon placed parallel to one another with the original outer surfaces in contact, while what was previously the inner surface is directed outwards. In this position the two halves are firmly tied together by string at their two ends. If the two pieces thus joined are placed in water, they will in the space of a few minutes, as they again become turgid, arch apart so as to leave a wide aperture between them—in other words, the pore of our artificial stoma opens. A return to the salt-solution will once more result in a closure, and this sequence of events can be repeated several times.

If the artificial stoma, with the pore widely open, is for some time allowed to dry slowly by exposure to the air, a marked decrease in the width of the opening becomes apparent. The opening and closing of this model is due to the greater extensibility of the side away from the pore, just as in the actual stoma a difference in stretching power between the two sides of the cells bounding the aperture is in part responsible for the alterations in its width.

Not uncommonly a few, or even many, of the epidermal cells (cf. Fig. 57) grow out into more or less elongated, often branched, processes called *hairs*, which are especially common on leaves and, when numerous, are very obvious to the naked eye. They may remain unicellular (Fig. 63, B, C), or become multicellular (Fig. 63, D) by the formation of septa.

One of the most important *functions* of hairs, when numerous, is to bring about a decrease in the rate of transpiration. The moist air entangled between these hairs is sheltered from the wind, so that it is not readily removed by air-currents, nor does it diffuse rapidly into the dry atmosphere around. As a result of the presence of this moisture-laden air in the immediate neighbourhood of the leaf-surface, transpiration of water-vapour from the interior through the stomata is retarded. These *covering hairs* are usually dead and, at maturity, occupied only by air; such dead hairs often appear white, showing that a large proportion of the light falling upon them is totally reflected, hence they also afford protection against the heating effect of the sun and against excessive illumination. Hairs thus serve to reduce transpiration and act as a screen to the underlying chloroplasts.

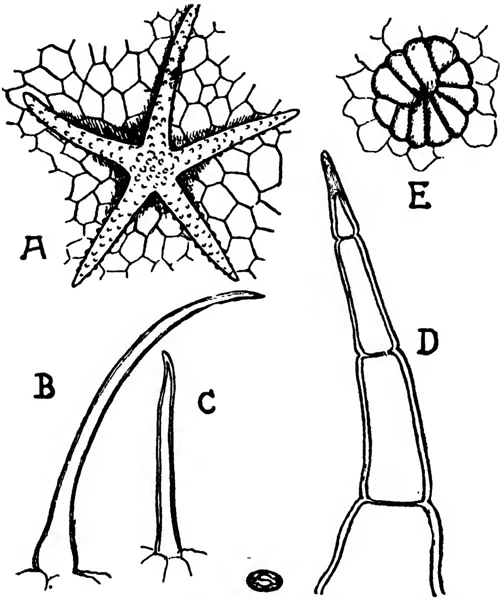

Fig. 63.—Hairs. A, of *Deutzia*; B, of *Cynoglossum*; C, of Shepherd's Purse (*Capsella*) (unbranched type); D, of Vegetable Marrow (*Cucurbita*); E, of Hop (*Humulus*).

Not uncommonly hairs are only present on the young leaf, falling off as the latter matures (*e.g.* Plane, Horse Chestnut, etc.).

Hairs, when their walls are thick and rough, not uncommonly act as a deterrent to animal attacks. A particularly striking example is furnished by the unicellular *stinging hairs* of the Nettle (*Urtica*) (Fig. 64, D). Each is borne on a multicellular stalk in which is embedded the thin-walled swollen base of the actual stinging hair. The upper part of the latter is comparatively thick-walled and tapers gradually to near the apex, where it suddenly enlarges to form a tiny bead-like tip (Fig. 64, E). The lower part of the wall is calcified, the upper part silicified. The living protoplasmic contents often show distinct streaming movements, and include a large vacuole filled with acrid sap. When an animal brushes against one of these hairs, the little tip breaks off, leaving exposed a fine needle-like point formed by the upper tapering part of the hair. As a result of the pressure of contact, this fine tube penetrates the skin, and the compression of the bladder-like base injects the contained fluid into the wound.

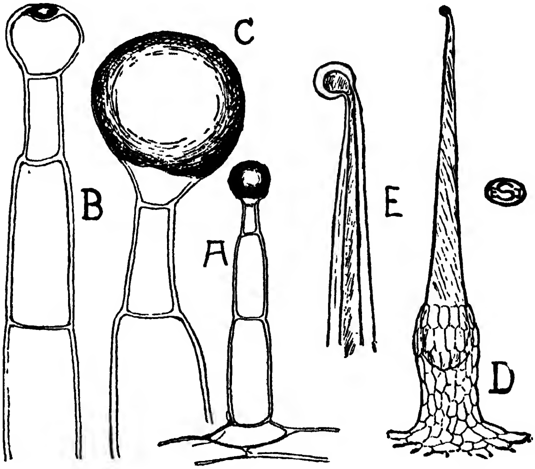

FIG. 64.—Glandular hairs of Chinese Primrose (*Primula sinensis*, A–C) and Stinging Hair of Nettle (*Urtica*, D, E). In A–C the secretion is shaded, and in C and E only the greatly magnified tip of the hair is shown.

The hairs of many plants produce secretions which are often of the nature of ethereal oils (cf. p. 108). Such *glandular hairs* are multicellular and generally consist of a basal cell, which is usually sunk in the epidermis, a projecting stalk, and a glandular head, but are otherwise of very diverse form. In the case of the Chinese Primrose (*Primula sinensis*, Fig. 64, A–C) and the

Garden Geranium (*Pelargonium*), the head is formed by a single cell and the stalk by a varying number of cells. In the Labiatæ (*e.g.* White Deadnettle) the head is composed of four or more cells disposed in a plane parallel to the surface of the leaf.

All the cells of such glandular hairs are living, those of the head which are concerned in active secretion being specially characterised by dense protoplasmic contents and large nuclei. Small droplets of secretion can often be recognised within the young glandular cells, but in the mature condition the ethereal oil is found deposited between the cuticle and the cellulose-layer of the outer wall (Fig. 64, B), so that after solution of the oil by means of alcohol a space is evident beneath the cuticle. The volatile oils produced by these glands are the cause of the fragrant perfume of many herbs (*e.g.* Lavender), and in some cases play a part in the reduction of transpiration (cf p. 110) or render the plants distasteful to animals.

Insects are most commonly attracted to flowers by nectar formed in special structures termed *nectaries* (cf. p. 287). The honey is produced by the active secretion of cells belonging either to the modified epidermis or to the underlying tissue. The nectary of the Hogweed or other common member of Umbelliferæ, found on the top of the ovary, is seen in a cross-section to consist of a mass of small glandular cells having the customary thin walls, abundant protoplasm, and large nuclei, and covered by an epidermis containing numerous stomata.

In all nectaries it is primarily the secretion of osmotic substances on the surface (largely sugars) which initiates the exudation of liquid, and the mechanism can be well imitated by scooping out two hollows in an unpeeled Potato and filling one of them with powdered sugar. After about an hour the latter cavity will be found full of syrup which may even overflow, whilst the other is dry and empty. The sugar has drawn water out of the cells of the Potato in much the same way as the root-hairs take up moisture from the soil.

CHAPTER XIV

THE STRUCTURE OF THE LEAF

THE blade of a dorsiventral foliage leaf exhibits the following general structure in transverse section. Beneath the colourless epidermis (Fig. 65, *Ep.*) of the upper side are one or more layers of vertically elongated cells constituting the *palisade tissue* (*Pa.*), which is especially concerned with carbon dioxide assimilation; its cells are deep green owing to the numerous chloroplasts. Between the palisade layer and the lower epidermis lies the loose "*spongy*" *tissue* (*Sp.*), which is composed of irregular cells separated by many and often conspicuous intercellular spaces (*In.*). This tissue contains fewer chloroplasts and communicates with the external atmosphere by way of the stomata, its chief function being to facilitate gaseous exchange. Palisade and spongy tissues together constitute the thin-walled ground-tissue, or *mesophyll*, of the leaf. Here and there the section will pass through *veins*, some cut transversely, others obliquely or longitudinally; the veins include the vascular tissue with xylem towards the upper and phloem towards the lower side, and each is surrounded by a well-defined layer of cells, the *bundle-sheath* (*Sh.*).

Good material for a detailed study of the structure of an ordinary leaf is furnished by the *Fuchsia*. The features of the epidermis have been fully described in the previous chapter and require no further mention. The *palisade* cells are four to six times as long as broad and form a single layer (Fig. 65, *Pa.*). They are attached on the one hand to the upper epidermis, and on the other to the rounded cells constituting the uppermost layer of the spongy parenchyma. Narrow intercellular spaces, extending the whole depth of the palisade layer, occur at intervals between the cells, but these spaces are only apparent here and there

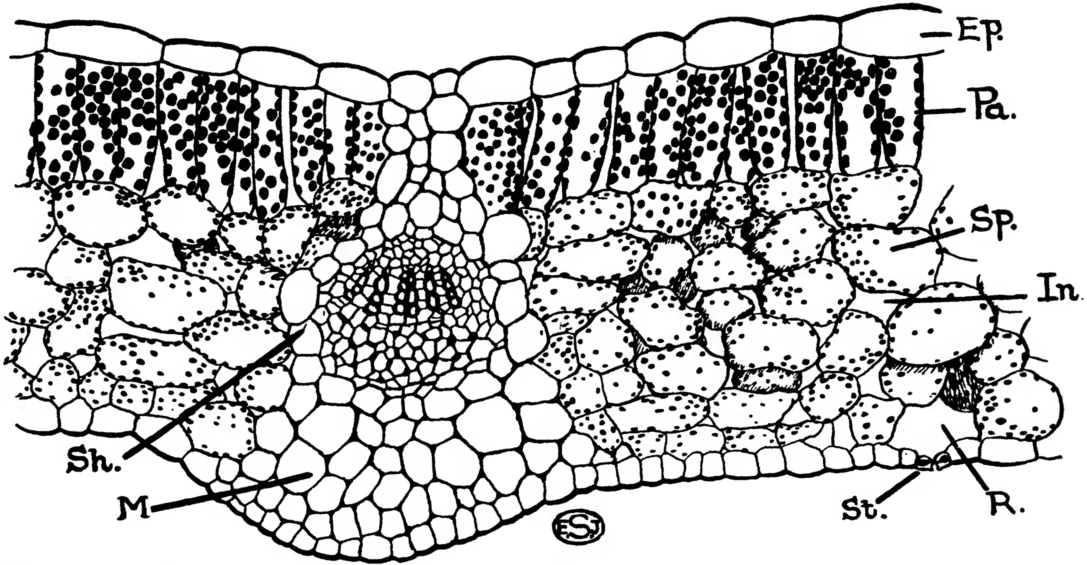

FIG. 65.—Transverse section of the leaf of *Fuchsia* passing through a vein. *Ep.*, epidermis ; *In.*, intercellular space ; *M.*, collenchyma of the midrib ; *Pa.*, palisade layer ; *R.*, respiratory cavity ; *Sh.*, sheath of vascular bundle ; *Sp.*, spongy parenchyma ; *St.*, stoma.

in the transverse section (cf. Fig. 65, *Pa.*). In sections parallel to the surface of the leaf the palisade cells appear rounded (being cut transversely, Fig. 66, A), so that they have the form of a number of closely packed cylinders placed side by side and interspersed with regularly disposed vertical spaces (*i.p.*), where the curved surfaces are not in contact.

The numerous lenticular *chloroplasts*[1] form an almost continuous layer in the cytoplasm lining the vertical walls, a feature well seen in both transverse and surface sections (Fig. 65, *Pa.*; Fig. 66, A: chloroplasts shown black). This peripheral position is clearly favourable to the rapid absorption of carbon dioxide from the adjacent intercellular spaces. Moreover the chloroplasts, as a result, present their edges to the light so that the chlorophyll

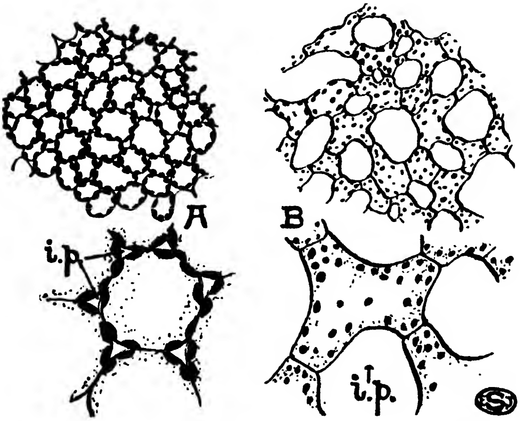

FIG. 66.—Sections parallel to the surfaces of a *Fuchsia* leaf, cut respectively through the palisade layer (A) and through the spongy parenchyma (B). In each case the lower figure shows a small portion on an enlarged scale. *i.p.*, intercellular spaces.

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[1] For the general properties of *chlorophyll*, see later, p. 170. It is now known that the chloroplasts of all plants contain two green (chlorophyll *a* and chlorophyll *b*) and two yellow pigments (carotin and xanthophyll), the former being present in considerably greater quantity than the latter. The chlorophylls, which differ but slightly from each other, are complex compounds of Carbon, Hydrogen, Oxygen, Nitrogen, and Magnesium, whilst the yellow pigments are of simpler composition; carotin has the formula $C_{40}H_{56}$, and xanthophyll the formula $C_{40}H_{56}O_2$. A rough separation of the green and yellow pigments may be effected by shaking up an alcoholic extract with benzol and allowing the liquids to settle; the alcohol then contains the yellow, the benzol floating above it the green, pigments.

is protected from the injurious effects of intense illumination. Owing to the considerable length of the palisade cells, there is accommodation for a large number of chloroplasts in each.

In the transverse section of the leaf of the *Fuchsia* two or three palisade cells frequently join by their lower ends on to one and the same cell of the spongy parenchyma (Fig. 65). The cells in question are usually broadened at their upper ends, so that they are more or less funnel-shaped. It is probable that the assimilation-products (carbohydrates, etc.) formed in the palisade cells pass into these *collecting cells* and from them diffuse, via other spongy elements, to the veins.

The *spongy parenchyma*, in its most typical form, consists of irregularly lobed cells attached to one another by their projecting arms (cf. Fig. 66, B), so that wide intercellular spaces occur between them. There are rather few chloroplasts in the spongy, as compared with the palisade, parenchyma, and this may be related to the fact that the former tissue receives relatively little light. The chief function of the spongy tissue is to constitute an extensive intercellular system communicating on the one hand with the atmosphere by way of the stomata, and on the other hand with the entire aerating system of the rest of the plant (cf. p. 189). The spongy cells also serve to conduct elaborated food-materials in various directions to the adjacent veins, a function for which they are well suited by virtue of their irregular shape.

The *vascular tissue* of the leaf is very extensive, forming an irregular network in Dicotyledons and a very regular parallel system in most Monocotyledons. The repeated branching facilitates not only the delivery of water and mineral salts to all parts of the leaf, but also the rapid removal of elaborated food-substances. This vascular system, however, also constitutes a supporting skeleton for the lamina, in which it is often aided by accompanying mechanical tissues; the latter are found especially in the larger veins, and consist of strands of collenchyma (Fig. 65, *M.*) or sclerenchyma, which run both above and below the vascular bundles or sometimes on the lower side only.

A transverse section through one of the principal veins of the *Fuchsia*-leaf shows a single collateral bundle (cf. p. 119) enveloped in a sheath of one or more layers of large transparent thin-walled parenchyma-cells (Fig. 65, *Sh.*); the accompanying collenchyma (*M.*) is developed especially on the lower side. The xylem, which is adjacent to the palisade tissue, consists of rows of vessels alternating with wood-parenchyma, the protoxylem being directed towards the upper epidermis; the phloem is of the normal type and lies towards the lower side, although the midrib is bicollateral. Between xylem and phloem a cambium can often be recognised (Fig. 65), especially in evergreen leaves (*e.g.* Holly) which remain on the plant for more than one year. In passing to the finer and finer ramifications of the vascular system a gradual simplification in structure is apparent.

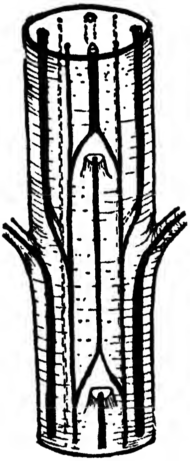

FIG. 67.—Diagrammatic representation of the vascular system in a small portion of the stem of the Mouse-ear Chickweed (*Cerastium*) (modified from Prantl). Only the bases of the leaves, with a single vascular strand, are shown.

In larger leaves (*e.g.* Sunflower) the *midrib* often contains several bundles. The vascular supply is in general proportional to the size of the leaf, and this is true also of that of the *petiole.*

The bundles of the latter can be traced backwards some little distance into the cortex of the stem, following a slightly oblique course, so that, in sections cut transversely just below the nodes, the one or more bundles passing from the leaf into the stem appear cut obliquely in the cortex. After penetrating some little way into the latter the bundles turn abruptly downwards and run vertically through one or more internodes, ultimately, with (Fig. 67) or without previous branching, fusing laterally with strands derived from other leaves. The bundles traversing the stem are therefore merely downward continuations of those found in the leaves.

The customary disposition of the *mechanical elements* (vascular bundles) in petiole and midrib is in the form of an arc with the opening towards the upper surface. This admits of considerable flexibility under the influence of wind, etc., but at the same time is well suited to withstand the vertical strain caused by the weight of the leaf-blade.

CHAPTER XV

SECONDARY THICKENING

IT has been pointed out that the vascular supply of the leaf is roughly proportional to its size (p. 140), and similarly the vascular system of the stem is correlated with the area of leaf-surface which it bears. With the annual increase of foliage exhibited by all woody perennials, a need for additional conducting elements arises, and this want is supplied through the activity of a meristem (the cambium, p. 122) which, in all Dicotyledons and Conifers, is situated between the xylem and phloem of the bundles. The division of the cells of the cambium leads to the formation of additional conducting elements, accompanied by a gradual increase in the size of the stem, spoken of as *secondary thickening.*

The cambium may be regarded as arising from a layer of undifferentiated cells, which has retained its powers of division, but it is difficult to recognise until it becomes active. In this layer of cells divisions take place parallel to the two tangential faces whereby files of segments are produced, both on the outer and inner side, those adjacent to the phloem becoming differentiated as additional (secondary) phloem, those adjacent to the xylem as additional (secondary) xylem.

Subsequently a similar division by two parallel tangential walls takes place in certain of the cells of the rays, so that a cambium between the bundles (*interfascicular,* Fig. 68, *I.c.*) links up with that within the bundles (*intrafascicular,* Fig. 68, *C.*) to form a complete cambial ring. The subsequent division of the interfascicular cambium is like that of the intrafascicular, so that the whole cambial cylinder cuts off segments on both sides. In some plants, however, there is a complete cambial cylinder from early stages onwards. In woody perennials the cambium resumes its function each year, although division is arrested during the winter months (cf. below).

The secondary wood thus added on the inside forms a larger and larger core each year (Fig. 69, A). Since it is composed of hard persistent tissue, there is practically no compression of the wood, which progressively accumulates, so that the increase in girth of the stem serves as a rough measure of the amount of tissue added. To this enlargement the secondary phloem contributes but little, since this tissue is mainly thin-walled, and the outer earlier-formed elements become compressed more and more, as a consequence of the increasing pressure resulting from the growth of the wood and the annual formation of intercalated phloem. The cambium keeps pace with the enlargement of the

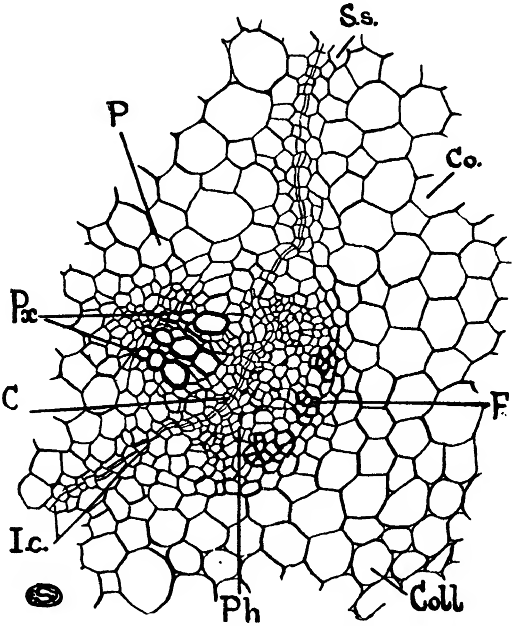

FIG. 68.—Transverse section of a small portion of the hypocotyl of the Castor Oil plant (*Ricinus communis*). *C.*, intrafascicular cambium; *Co.*, cortex; *Coll.*, collenchyma; *F.*, pericyclic fibres; *I.c.*, interfascicular cambium; *P.*, parenchyma; *Ph.*, phloem; *Px.*, protoxylem; *S.s.*, starch sheath.

circumference of the secondary wood by tangential stretching and occasional radial divisions in its cells.

The pressure on the outer tissues, due to the *interpolation of secondary vascular elements* between the primary xylem and phloem, becomes more and more marked as the years go by and its effects are most pronounced in the cortex. Moreover, the steady increase in size of the woody core results in a gradual enlargement of its circumference, so that the softer tissues beyond become tangentially stretched. This tension can be readily demonstrated by making an extended vertical incision through the cortex of a three-year-old twig of the Ash. The edges of the cut are seen to separate immediately owing to transverse contraction of the thin-walled tissues. In nature the tangential

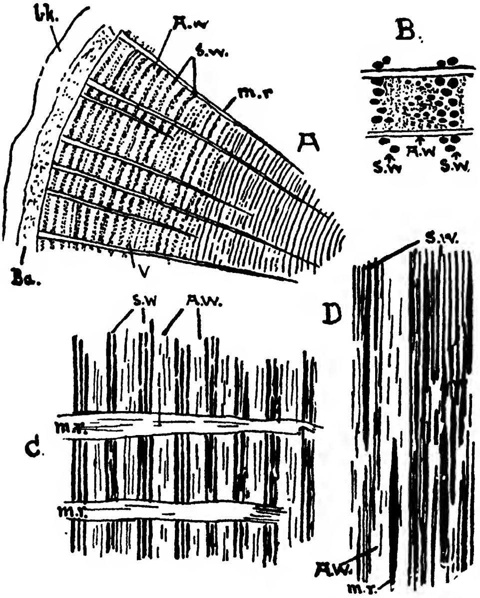

FIG. 69.—Structure of a woody trunk (somewhat enlarged). A, Portion of a cross-section. B, Small part of wood of same, more enlarged. C, Radial longitudinal section of the wood. D, Tangential longitudinal section of wood. *A.W.*, autumn-wood; *Ba.* secondary phloem; *bk*, bark; *m.r.*, parenchyma rays; *S.W.*, spring-wood; *V*, vessels.

tension is exemplified by the irregular longitudinal fissures which are so marked a feature of the older bark of many trees.

At certain points, where the cambium consists of isodiametric cells, the segments cut off are parenchymatous and differ from the other elements of the wood and phloem in being radially and not longitudinally elongated (Fig. 70, A.). In transverse sections of a secondarily thickened stem these *parenchyma rays* appear as a number of radiating streaks, one or more cells in width (Fig. 69, A, *m.r.*). Some of these rays extend from cortex to pith and, since they correspond in position to the original rays between the vascular bundles, are called *primary* (*medullary*) rays; others (the *secondary* parenchyma rays), however, though traversing the greater part of the secondary phloem, penetrate only to a varying depth into the secondary wood.

The *secondary wood* is composed of four main types of elements, viz. vessels, tracheids, wood-fibres, and wood-parenchyma.

The *vessels* of the secondary wood usually bear densely crowded bordered pits (Fig. 70, *V*; Fig. 42, E. *b*, p. 89), often arranged in distinct vertical series. *Tracheids* differ from vessels in being derived from single segments of the cambium, which show no open perforations in the end-walls; they are usually much shorter than the vessels, but of about the same width. The vessels and tracheids are the water-conducting elements of the secondary wood, and the former are generally much more numerous than the latter. The typical *wood-fibres* closely resemble those described on p. 88, having pointed ends and more or less thickened walls (Fig. 70, *f*).

The *wood-parenchyma* cells of the secondary xylem resemble those of the primary xylem in form and in the possession of a living protoplast; the walls are, however, commonly thicker and often lignified, the horizontal ones showing prominent pitting (Fig. 70, *p*).

The structure of the *parenchyma rays* can only be fully appreciated by a study of their appearance in transverse, radial, and tangential longitudinal sections (cf. Fig. 69). In the transverse section the cells, except for the fact that their long axis is placed radially and not vertically, are very similar to those of the wood-parenchyma, though not uncommonly having somewhat thinner walls. The latter bear simple pits which are often particularly

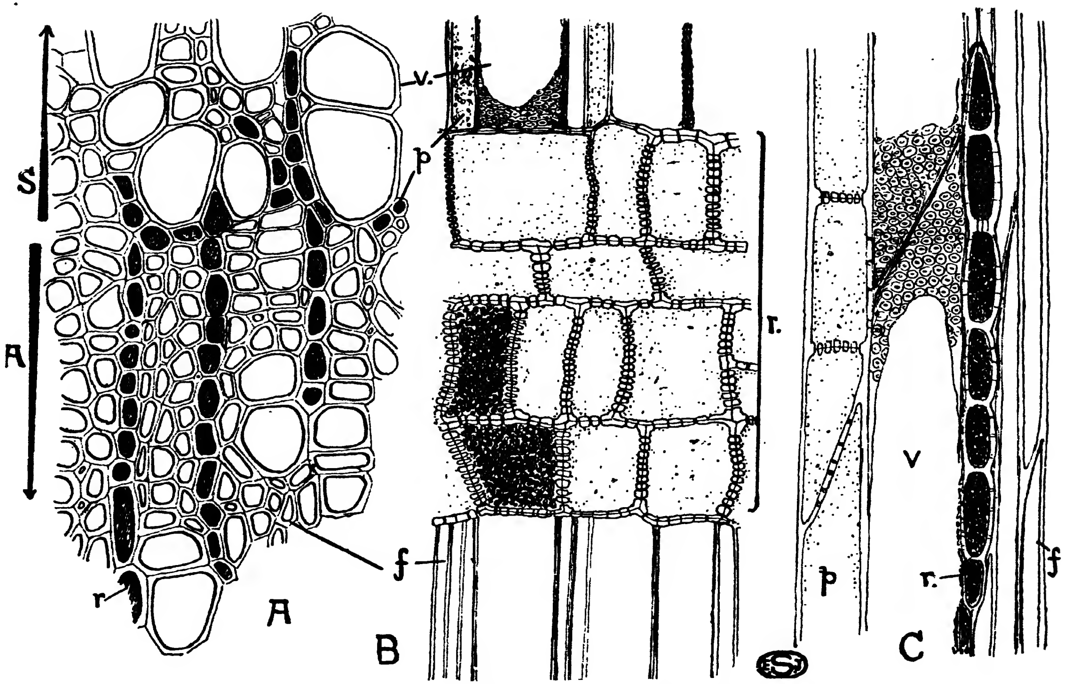

FIG. 70.—Structure of the secondary wood of the Horse Chestnut (*Æsculus*). A, Transverse section showing the spring-wood (*S.*) of one, and the autumn-wood (*A.*) of the preceding annual ring. B, Radial longitudinal section. C, Tangential longitudinal section. *f*, fibres; *r.*, parenchyma rays; *p*, wood parenchyma; *V*, pitted vessels of secondary xylem.

numerous on the tangential walls (Fig. 70, B). Each ray is a plate of cells of which the full vertical extent is seen in tangential longitudinal sections (Fig. 69, D; Fig. 70, C, *r*.). The secondary medullary rays are very limited in this direction, rarely exceeding ten or twelve cells in height, whilst the primary rays usually extend through an entire internode. Each ray, as seen in tangential section, is somewhat spindle-shaped as a result of the tapering of the cells at the upper and lower margins (Fig. 70, C, *r*.).

In radial longitudinal sections the secondary rays are cut parallel to their flat faces, and appear as so many narrow parenchymatous strips passing at right-angles across the longitudinal grain of the wood (Fig. 69, C; Fig. 70, B). The detailed structure of the ray here somewhat resembles that of a brick wall, the alternation of the cells simulating the " bond " of the bricks. The component cells show plainly the radial elongation referred to above. The radial, like the vertical, extent of the secondary rays is seen to be limited (cf. p. 144), the rays penetrating inwards from the cambium for varying distances. Should the radial section pass through one of the primary rays, the latter will be seen to show a far greater development, both in the vertical and radial directions.

Apart from the occasional presence of fibres with protoplasmic contents, the wood-parenchyma and the parenchyma rays are the only living constituents of the secondary wood. The living cylinder constituted by the phloem and cortex is thus connected with numerous inwardly directed plates of living tissue, the parenchyma rays. Of these, however, only the primary ones extend to the pith, where they are linked up by a second cylinder of living cells, the *medullary sheath* (p. 123), which invests the inner margins of the primary xylem strands. The radiating plates formed by the secondary parenchyma rays are, however, not isolated, even where they pass between the dead elements of the secondary wood, since they are connected both vertically and horizontally by bands of wood-parenchyma cells.

The mass of vessels and fibres is thus permeated by a continuous system of living elements connected with the food-conducting tissues. The functions of this system are twofold: firstly, to conduct elaborated food-substances to the cambial region, the living cells of the wood, and the medullary sheath; secondly, at certain times of the year (cf. p. 18), the cells serve for the *storage* of food-substances, *e.g.* starch, as can be shown by the application of iodine to a section of a twig in autumn. When this starch is utilised during the sprouting of the buds in spring, it is changed into sugar, and is then transferred in the water ascending the vessels to the growing regions, hence the sweet character of the sap which exudes in bleeding (cf. p. 157). The aeration of the secondary tissues is effected by narrow intercellular spaces which are more particularly associated with the living elements.

The major part of each annual addition to the secondary wood usually consists of vessels and fibres, but the proportion of these latter varies with the kind of plant and during each season's growth. The wood formed in the spring (*spring-wood*, Fig. 70, A, *S.*; Fig. 69, A, *S.W.*) mostly contains a much larger percentage of vessels than that produced later (*autumn-wood*, *A.*); its vessels, moreover, are often larger and have thinner walls, and the same may be true of the fibres. This difference can be related to the sudden demand on the water-supply in the spring on the part of the newly expanding leaves, whilst later in the season provision can be made for the growing mechanical requirements of the plant by an increased proportion of fibres. As a consequence there is a sharp boundary between the dense small-celled autumn-wood of one season and the wide-celled spring-wood of the next (Fig. 70), and this leads to the marking out of the secondary wood into a succession of *annual rings* (Fig. 69, A), by means of which the approximate age of a trunk can be estimated. Occasionally, however—as, for example, when a new set of leaves is produced to replace a first crop killed by frost or devoured by caterpillars—their expansion is accompanied by the formation of a second zone of spring-wood, so that two "annual rings" are formed in a single season.

The constant addition of new wood is probably mainly necessitated by changes in the central earlier-formed xylem, as a result of which it becomes useless for purposes of conduction, although such changes often increase its value as a mechanical support; it is then spoken of as *heart-wood* in contrast to the active *sap-wood* beyond. The elements of the heart-wood often become impregnated with tannins, resins, etc., which are frequently accompanied by dark-coloured pigments. The impregnating substances are often antiseptic, and prevent decay by inhibiting the development of Fungi and Bacteria, thus increasing the durability of the wood. Teak (*Tectona grandis*) owes its great value as a tropical timber to the presence of an oil which renders it immune from the depredations of wood-boring insects; it is also the cause of its peculiar scent. The liability of many Willows to develop hollow trunks at an early stage may be attributed to the absence of antiseptic substances from the heart-wood.

Most of the gross features of timber above described can be recognised by examination of appropriate surfaces with a hand-lens (cf. Fig. 69). The mechanical properties of timbers depend largely on the proportion of fibres, on the number and size of the vessels, and on the thickness of the fibre walls. The timbers commonly used for cabinet work (*e.g.* Mahogany, Ebony, Walnut, etc.) are the heart-woods of the respective plants.

The ***secondary***, like the primary, ***phloem*** is composed of sieve-tubes, companion cells, and phloem-parenchyma, often accompanied by fibres, and these are not infrequently produced in alternating tangential bands. The parenchyma rays of the secondary phloem are continuous with those of the xylem and exhibit the same general structure, except that the component cells remain thin-walled.

A transverse section of any unthickened Dicotyledonous ***root*** will show a narrow band of two or three layers of parenchymatous cells between each phloem-group and the adjacent xylem. Prior to the commencement of secondary growth tangential division-walls arise in these cells, leading to the production of a ***cambium*** (Fig. 52, *ca.*, p. 114) like that of the stem. In this way there originate as many cambial strips (Fig. 63, A, B, *C.*) as there are groups of phloem, and, by the active division of the former, secondary xylem is produced on the inside and secondary phloem on the outside. Differentiation of the cambium is at first confined to the inner surface of each phloem-group, but by slow degrees it extends along the sides of the xylem-arms till finally, by the development of tangential division-walls in the cells of the pericycle opposite the protoxylems, a complete lobed cylinder of cambium is established. Owing to the late development of the cambium opposite the protoxylem - groups, secondary thickening is at first more extensive in the bays, so that the outline of the cambium, at first lobed, gradually becomes circular.

The root soon comes to possess a broad ring of secondary wood and phloem (Fig. 71, C), similar to that of the stem, and, as in the latter, traversed by primary (*P.r.*) and secondary *rays*. Old, secondarily thickened roots resemble stems very closely; but, when the central tissues are preserved, the original root-structure can be traced by following down the primary rays and locating the protoxylem-groups at the periphery of the metaxylem.

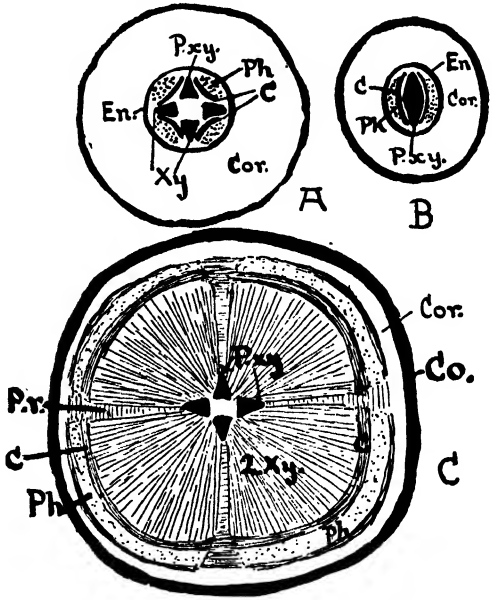

FIG. 71.—Diagrams showing secondary thickening in the root. A, a tetrarch, and B, a diarch root, before thickening, showing the position of the cambium (*C.*). C, a tetrarch root after secondary thickening has been going on for some time. *Co.*, cork; *Cor.*, cortex; *En.*, endodermis; *Ph.*, phloem; *P.r.*, primary ray; *P.xy.*, protoxylem; *Xy.*, primary xylem; *2xy.*, secondary xylem.

One result of secondary thickening is a marked enlargement of the periphery of stem or root, in consequence of which the outer tissues are subjected to increasing tension (cf. p. 143). These, the epidermis and cortex, ordinarily have but a limited power of stretching, and, as soon as this limit is reached, they rupture and no longer form an effective covering for the underlying tissues. This function is henceforth fulfilled by a secondary protective tissue, the *cork*, formed by the active division of another cambium, the phellogen or cork-cambium, which arises somewhere in the cortex.

Cork-formation takes place in essentially the same way in both stem and root. The *phellogen* invariably arises by the development of two successive tangential walls, in the case of the stem most commonly in the cells of the subepidermal layer (Fig. 72). The cells are thus each divided into three segments, of which the central constitute the actual cork-cambium (*c.c.*), whilst the outer form the first layer of cork and the inner the first, and often the only, layer of a tissue known as *phelloderm* (*Ph.*). Whilst the outer and inner segments undergo no further division, the cells of the phellogen divide again and again, one of the two products of each division becoming differentiated as cork or phelloderm, while the other remains as the cell of the cork-cambium. In

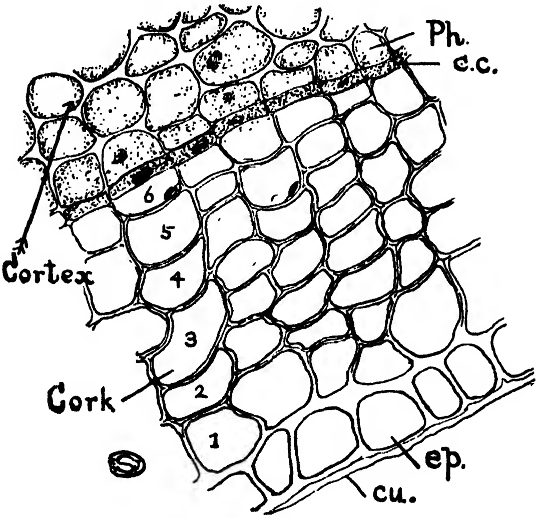

Fig. 72.—Transverse section through the cork layer in the stem of the Elder (*Sambucus*). *c.c.*, cork-cambium; *cu.*, cuticle; *ep.*, epidermis; *Ph.*, phelloderm; 1–6, successive segments of the cork in order of production.

the majority of cases, however, these divisions of the phellogen lead to the cutting-off of cells on the outside only, so that no further formation of phelloderm takes place. Sometimes the cork arises in a much deeper-seated layer, as is almost invariably the case in roots.

The activity of the cork-cambium results in the development of a continuous tissue consisting of numerous radial files of cells, each file (Fig. 72, 1–6) representing the product of one cork-cambium cell. This tissue is the cork and, apart from the absence of intercellular spaces between its cells, it is especially characterised by a chemical modification of the cell-walls spoken of as *suberisation*. This latter renders them practically impervious alike to gases and to liquids, features to which cork owes its utilisation in closing bottles.

Suberisation is due to the deposition of a layer of fatty compounds on the inner surface of the wall, and hence the cork is coloured by the same reagents (Scharlach red, etc.) as stain fats. A yellow-brown colouration is assumed with chlor-zinc-iodide, and a yellow one with strong potash. Suberised membranes, moreover, are highly resistant, being insoluble both in cuprammonia and concentrated sulphuric acid.

The cork not only prevents the excessive transpiration which would ensue from rupture of the epidermis consequent upon secondary thickening, but also takes over other protective functions of that tissue. Suberised walls possess considerable strength, though their elasticity is slight, and the cork consequently forms a mechanical envelope whose efficiency is heightened by the close connection between its cells. The frequent presence of air in the latter retards excessive heating by day or excessive cooling by night. Moreover, the waste substances commonly encountered in the walls or cavities of the cork-cells are antiseptic, excluding access of various parasites to the living tissues within. As soon as cork-development commences, therefore, the parts concerned become ensheathed in an almost impermeable protective layer which would practically sever all direct communication between the internal tissues and the atmosphere, but for the formation of localised patches of loose tissue, the *lenticels* (Fig. 21, 22), whose development often commences slightly before that of the cork.

The tissue of the lenticel is likewise formed from a cork-cambium, but the cells given off on the outer side remain thin-walled and unsuberised. They sooner or later round off and lose all connection with one another. This loose tissue is formed in considerable bulk, so that it leads to a gradual elevation and ultimate rupture of the overlying epidermis. The tissue of the lenticel is thus exposed, and air from the surrounding atmosphere can freely circulate between its cells and, by way of the narrow air-spaces between the cells of the phellogen and phelloderm, into the intercellular spaces of the cortex.

The dead tissues, on the outside of the cork, are shed sooner or later, leaving the latter exposed as *bark*. In most woody plants the first-formed phellogen ceases to divide, and indeed itself becomes changed into a layer of cork, at a comparatively early stage. A new cambium then arises at a deeper level in the cortex, produces a fresh zone of cork, and then in its turn passes out of action, to be succeeded by another situated still deeper. The bark formed in this way consists of alternating layers of cork and dead cortex, and comprises all the tissues beyond the most recently established phellogen.

It will have become apparent that cork serves to protect surfaces which would otherwise be exposed, and indeed it is even found covering wounds and scars left by the shedding of leaves, flowers, branches, etc.

CHAPTER XVI

THE PLANT IN RELATION TO ITS WATER-SUPPLY

IT has been repeatedly stated that the root-hairs are the organs by means of which water is absorbed from the soil,[1] but the way in which this is effected remains to be studied. It will help us in the first place to perform a simple experiment.

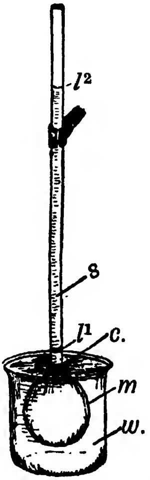

FIG. 73.—Demonstration of osmosis (Osterhout's method). *m*, egg-membrane; l^1, l^2, the successive levels of the sugar-solution. For other lettering, see text.

A small hole, about one-fifth of an inch across, is pierced through the pointed end of a number of eggs and the contents blown out by means of a fine glass tube. The shells are then

[1] An experiment to prove that water is absorbed by roots was described in Chapter I (p. 8).

placed singly in cups filled with a weak solution of vinegar in water; this will gradually dissolve away the calcareous shell, leaving only the delicate membrane which lines its inner surface. A piece of glass tubing, about 8 inches long, is inserted through the hole in each membrane and the edge of the latter is bound tightly with cotton round the end of the tube (Fig. 73, *c*). The empty membrane is then completely filled with a strong sugar-solution (about 10 per cent.) till this rises about a quarter of an inch up the tube (Fig. 73, l^1). Thereupon the whole is fixed in such a way that the membrane (*m*) is completely immersed in a tumbler of water (*w*), and the level of the sugar-solution marked by a strip of gummed paper (l^1). After a short time the liquid in the tube will be found to have risen, and this continues till ultimately the whole tube is nearly full (l^2). Occasionally the membrane leaks, and therefore it is advisable to set up several experiments.

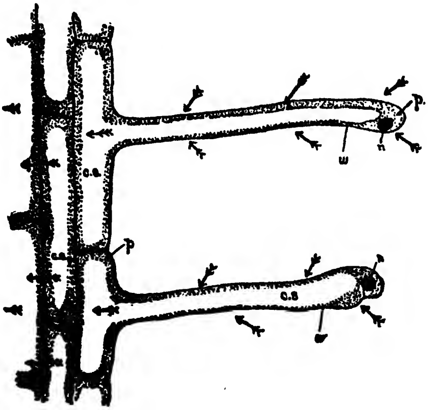

FIG. 74.—Diagram of surface-cells of root with two root-hairs (very considerably magnified). The direction taken by the water is indicated by arrows. *c.s.*, cell-sap; *n*, nucleus; *p*, protoplasm; *w*, cell-wall.

We can conclude that water has passed by osmosis (cf. p. 63) through the semi-permeable membrane into the sugar-solution and has thus brought about the change in level observed. If we could substitute for the egg-membrane and sugar-solution a root-hair or other living cell of the plant, the same result would be obtained. In the case of the root-hair a weak solution, the soil-water, and a relatively strong one, the cell-sap (Fig. 74, *c. s.*), are separated by the cell-wall (*w*) and the cytoplasmic layer (*p*) lining the inner surface of the latter; the conditions for an osmotic flow are thus given.

The water around the contiguous soil-particles is thus continually being drawn into the root-hairs and, in its place, further moisture flows in from the surrounding soil; the cell-sap of the root-hair thus becomes diluted (*i.e.* weaker than that of the cells lying beneath the piliferous layer), so that the water will begin to flow inwards by osmosis (see the arrows in Fig. 74). In this way it gradually moves towards the centre of the root and thus ultimately reaches the xylem-groups, whence it passes to the stem and leaves. It may be added that the exact way in which the transference to the wood takes place is not yet fully understood.

We have seen that the turgid character of living cells (p. 64), when in a healthy condition, is due to the attraction of water into the cell-sap till this distends the cell-walls and the underlying cytoplasm to their utmost limit. This can be illustrated by filling an egg-membrane, obtained as above, with strong sugar solution and, after securely tying up the opening, placing it in a vessel of water. The membrane, which at first is flabby, gradually becomes more and more distended as water is taken up, *i.e.* it becomes firm and turgid.

The woody strands in the young shoots of trees and shrubs and in the stems of most herbs are by themselves insufficient to bear the strain, even of the plant's own weight. This is readily seen when plants in a vase droop for want of water, but again become erect when a fresh supply is added; and the same observation can be made in nature on any hot summer's day. The plant being largely composed of turgid cells, the whole (*i.e.* root, stem and leaves alike) forms a stiff structure which only becomes flaccid when water is lost. Part of the liquid can be readily withdrawn from the turgid cells by placing herbaceous plants (*e.g.* any seedling) in a strong solution of salt for some minutes, when they become quite limp, though subsequent immersion in water restores the original turgidity.

There is a further aspect of turgidity that plays an important part in the stability of the herbaceous plant. To study this point we select young shoots of the Elder (or in winter the flowering stems of Narcissus or Daffodil) and cut off a piece about 8 inches long with straight ends. The hard outer portion is then completely removed in four longitudinal strips leaving only the juicy central pith of the stem. If we now compare the length of the original piece with that of one of the outside strips and with that of the pith, we shall find that the former is a little shorter and the latter slightly longer. This indicates that in such a stem the pith is in a state of compression, whilst the outer tissues are in a state of tension. The advantage of this condition can be shown in the following way.

A weak spiral spring (such as can be made by twisting thin steel wire round a piece of wood), about 8 or 9 inches long, and a similar length of an inner tube of a cycle-tyre are obtained. Neither is capable of supporting itself in an erect position; if, however, the spring is slipped into the rubber tube and the former slightly compressed, so that the ends of the tube can be firmly tied, the two combined form a structure of considerable rigidity. Here, just as in the stem, the inner part is in a state of compression while the outer is extended.

It is in consequence of such tissue-tensions that many herbaceous shoots, when halved lengthwise, exhibit a curvature of the two halves with the exterior on the concave and the interior on the convex side; similarly the cut ends of the flowering stalks of Dandelions, when kept in water, split from below upwards into two or more portions, each coiling up like a watch-spring, with the inner side facing outwards (cf. p. 67).

Returning to the absorption of moisture by the root, we have first to notice that under certain circumstances the water appears to be pumped into the wood with great vigour, so that a considerable upward pressure (so-called *root-pressure*) is manifest. This may be demonstrated in the following way (Fig. 75): The stem of the plant of a Fuchsia or Vegetable Marrow growing in a pot is cut off about 2 inches above the level of the soil. To the cut stump a piece of glass tubing (about a yard long) is firmly connected by a short length of rubber tube, both joints being wired on so as to make them air-tight. A small quantity of water is now poured into the tube and covered with a drop of oil to prevent evaporation, after which the level (l^1) is marked in the usual way. The soil is well watered and the whole is kept in a warm place. Very soon the liquid in the tube will begin to rise and, in the case of a sturdy plant, will not take long to reach the top.

It will be obvious that, when such root-pressure exists, it must help in forcing water up the stem, particularly when the latter is of no considerable height; an effective root-pressure is, however, in nature realised only at certain times (mainly in spring). Such pressure also finds expression in another way, viz. in the phenomenon of *bleeding*, in which the exuded liquid collects on the cut end of the stem, as is well seen in the Cress and in trees felled in spring.

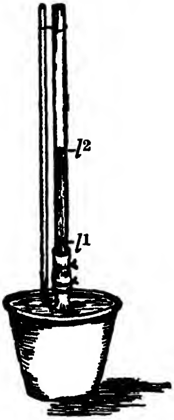

Fig. 75.—Demonstration of root-pressure, see text. l^1, l^2, the successive levels of the water-column.

It has already been shown (p. 8) that the woody strands are the channels through which the water passes, but a further proof is supplied by the fact that a ringed branch (*i.e.* one from which all the tissues outside the wood have been removed for a short distance) remains healthy for weeks, if left on the plant or kept in water under suitable conditions. In such a case the moisture can be travelling only through the wood or the central pith, but since the latter completely disappears from the mature stem of many plants it is obviously not essential for water-conduction.

That the vessels (p. 88) actually serve to convey the water can be shown as follows: Place the cut end of a healthy shoot for some minutes in butter, which is kept melted, and then put it aside to cool, so that the butter sucked up solidifies. The extreme end is next shaved off, which removes all the short elements (ground tissue, wood-parenchyma) that have become filled with butter, but not the elongated vessels. The shoot, together with another not thus treated, is thereupon placed in water. After some hours, whilst the latter is still fresh, the former has faded owing to the plugging up of its vessels.

Through the vessels the water ultimately flows into the leaves and from these, as we have already seen (p. 9), a great part is given off in the process of *transpiration*. The cobalt-method described on p. 9 will serve to show the occurrence of transpiration from any leaf. Another familiar demonstration is the collection of moisture on the inside of a bell-jar placed over a healthy plant, although in order to obtain a reliable result both pot and soil should be covered with some water-proof material (*e.g.* silver paper).

It was noticed in applying the cobalt-method to the Shepherd's-purse (p. 9) that transpiration was more rapid on the lower than on the upper side of the blade, and this would be found to be the case in very many (*e.g.* Lilac, Vine, Black Poplar), though not in all plants. Choosing two healthy leaves of the normal type, the ends of the petioles, and the lower and upper surfaces respectively, of the blade are covered with vaseline, after which the two are hung up in a warm room. A few hours later the blade vaselined on the upper surface will be more or less withered, whilst the other will have remained almost fresh. The latter result is due to the vaseline closing up the stomata through which the water-vapour chiefly escapes. The experiment again indicates that transpiration is most active on the lower surface and also demonstrates the importance of the stomata in this process.

Comparison of fresh and faded leaves of the same plant with the help of the cobalt-method shows that transpiration is slower in the wilted ones; this is largely due to increase in the concentration of the leaf-sap which causes a corresponding decrease in the rate of evaporation. A diminution in the size of the pores is also partly responsible, but complete closure occurs too late to be of avail. The pores remain wide open, when the guard-cells are turgid (p. 131), the usual condition in bright light, whilst at night the pores close.

We have, so far, only described methods of demonstrating transpiration, but an indirect measure of the rate of this process can be obtained with the help of an instrument known as a *potometer*. The shoots employed in experiments with this instrument should be removed from the plant some hours previously and kept in water; before use the lower 3 inches of the stem should be cut off previous to removal from the water. The potometer (Fig. 76) consists of a 2-oz. bottle with a wide neck, fitted with a three-holed rubber cork into the holes of which we insert respectively: (i) a cylindrical funnel (*a*) passing into a narrow glass tube provided with a stopcock (*b*); (ii) a piece of capillary tubing (*c*) bent once at right angles and with a scale attached to the horizontal arm; (iii) a piece of ordinary glass tubing (*d*) bent as shown in the Figure. To prepare the instrument for use the stopcock is opened and water is poured into the

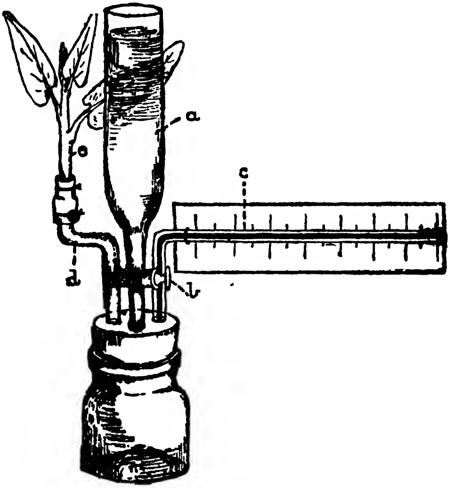

Fig. 76.—Potometer (Farmer's method). Full description in text.

funnel until it overflows from the ends of tubes *c* and *d*, whereupon *b* is closed.

A short length of rubber tubing is carefully passed over the end of a leafy shoot (see Appendix VII), and by this means the latter (*e*) is attached to the glass tube *d*, so that the end of the stem dips into the water; the connection is rendered air-tight by binding the rubber on to stem and tube respectively with wire. If the horizontal arm of the capillary tube *c* is carefully watched, a column of air, starting at the open end, will be seen to creep along it; this is due to the fact that the moisture lost in transpiration from the leaves is replaced by an almost equal amount taken up from the bottle. By opening the stopcock, until the column of air has been driven back, and again closing it, the potometer is prepared for a fresh observation; and, if we record (with the help of the seconds-hand of a watch) the time taken for the end of the air-column to pass over a measured distance on the scale, the average of several readings will give an estimate of the rate of transpiration from the shoot employed.

In this way we can determine and compare the rates of transpiration[1] from shoots of different plants, the contrast afforded by evergreen and deciduous types being specially instructive. Moreover, the potometer can be used to study various aspects of transpiration. If, for instance, half the leaves of a shoot are removed or vaselined, it will be found that, as a result of the reduced transpiring surface, the rate of absorption (as indicated by the movement of the air-column) is in either case much decreased. We may also compare shoots exposed to different conditions, such as a hot and a cold room, dry and moist air, moving air (*e.g.* a draught) and still air, and in each case we shall find that the first of the two alternatives induces more active transpiration. This process is therefore accelerated by heat, dryness of the air and wind.

The actual amount of transpiration in a given time can be measured by placing a potted plant (soil and pot being covered with waterproof material) on one scale-pan of a coarse balance and putting sufficient weights on the other to counterbalance it. After some time the scale-pan bearing the plant will be found

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[1] In reality of course the potometer measures the rate of absorption; but we may take it that this is proportional to the rate of transpiration.

to have risen, and by adding weights to it the amount lost in transpiration can be gauged. If a perfectly accurate result was required, it would be necessary to allow for the gain in weight as a result of assimilation and the loss due to respiration (cf. p. 192).

As a result of the giving off of moisture from the surface of the plant in transpiration, a marked suction is produced, which can be readily demonstrated by the experiment shown in Fig. 77, A. The end of a leafy shoot (cut under water, see p. 159, and with the surface of the stem vaselined) is firmly fixed by rubber tubing into the upper end of a long narrow glass tube filled with water, the lower end of the tube dipping into a vessel containing mercury. By slow degrees the mercury will be seen to rise in the tube, replacing the water sucked up by the shoot as a result of its transpiration. That this is a purely physical phenomenon can be shown by substituting some porous mass for the shoot. The bulb of a thistle funnel is *loosely* packed with wet Plaster of Paris (*p* in Fig. 77, B), which in setting will expand sufficiently to fill it completely. The stem of the thistle funnel is then filled with water and its lower end placed as before in mercury, when a similar gradual rise of the latter is observed. Experiments of this kind, carefully performed, have shown that the mercury will ascend to a considerably higher level than that supported by ordinary atmospheric pressure (viz. 30 inches).

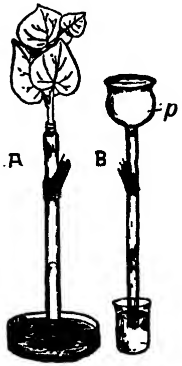

FIG. 77.—A, Demonstration of suction due to transpiration. B, Demonstration of suction due to evaporation from a porous mass (*p*). For details, see text.

It will be obvious that this suction must materially assist in the upward passage of water through the plant, but the entire mechanism of the ascent of sap is far from being properly understood, and involves such complicated principles that its consideration would be out of place in a book of this scope. When a plant is obtaining abundant moisture, so that absorption is in excess of transpiration (and it is at such times that root-pressure is generally to be observed), the water in the vessels is forced upwards under a positive pressure. As soon, however, as transpiration is only just balanced by absorption, the water in the vessels is being pulled up by suction, so that it is in a state of tension. Under these circumstances the water-column is interrupted by air-bubbles whose pressure is less than that of the atmosphere, *i.e.* we have a *negative pressure* which can be demonstrated as follows:

If the stem of a plant, which has recently been little watered, is cut across and water placed on the exposed surface of the stump, it will be eagerly sucked up. When the stem of such a plant is cut open under a solution of red ink or mercury, the liquid, on splitting up the stem, will be found to have penetrated into the vessels to a much greater distance than in the case of a plant which has been well watered.

It is a familiar fact that if plants are gathered on a hot summer's day, when a negative pressure is almost invariably realised, they often wither even though placed in water soon after. This is due to air being sucked up into the vessels, which consequently lose their power of conducting moisture. If two shoots are cut, one under water and the other in the air, from a plant in which negative pressure has been demonstrated, the two being afterwards placed in water, the former will remain fresh, whilst the latter soon fades. Hence the necessity of cutting shoots under water, if they are subsequently to be used for transpiration-experiments (cf. p. 159).

On damp warm nights, when abundant absorption results in a considerable positive pressure and the stomata are closed, the excess of moisture cannot be altogether removed by transpiration and in many plants escapes through special apertures (the *water-pores*), over which it frequently collects as small drops of liquid. These water-pores resemble stomata, but their pore is permanently open ; they are usually situated on the margins of the leaves, *e.g.* at the tip of the leaf in Grasses, or upon the leaf-teeth in the Marsh Marigold and Fuchsia. If any one of these plants, in a well-watered condition, is placed beneath a bell-jar in a warm moist atmosphere, the drops of liquid marking the positions of the pores soon appear. The water passed out through these apertures is not pure, but contains various substances in solution.

The details given above will have made it clear that plants absorb a far larger amount of moisture than they directly need, since most of it is given off again in the process of transpiration.

The stream of water serves to carry the mineral salts absorbed from the soil, but there is no direct relation between the quantity of water transported through the plant and the amount of mineral salts absorbed. Transpiration is a danger with which a plant has to cope, since for photosynthesis a large evaporating surface provided with pores must be exposed to the air, and this renders a heavy loss of moisture inevitable.

The ordinary annual or perennial herb grows under conditions in which the slight variations in the amount of water furnished by the soil are sufficiently compensated by changes in the suction exerted by the plant (p. 155). The leaves of such plants are thin and flexible, which is due to the outer epidermal walls being but little thickened and to the presence of but a thin cuticle, so that some slight evaporation takes place over the whole surface. The more strongly the cuticle is developed and the more leathery the texture of the leaf, the more completely is transpiration restricted to the pores of the stomata. Plants possessing such leaves (*e.g.* Bilberry, Sea Holly) can consequently thrive in drier situations than the others and also, in many cases (*e.g.* the evergreens noticed in Chapter II), are able to retain their foliage throughout the winter, when, as previously stated, absorption by the roots is often very slow (cf. p. 18). In extreme cases transpiration is still further reduced by various anatomical devices (*e.g.* sunken stomata, p. 130, hairs, p. 133, etc.).

Plants which grow in a variety of situations show considerable differences in the thickness of the cuticle. Thus, the leaves of the Bracken or Bilberry growing on an open heath will be found to be thick and leathery, whilst those of the same plants growing in the moist atmosphere of a wood are thin and flexible.

The deciduous plant has been seen to meet the conditions of drought in winter-time by shedding its leaves, except for the scales enveloping the buds—that is to say, the transpiring surface becomes greatly reduced. A similar reduction, though less extreme, is exhibited by many plants of dry localities throughout the year. In the simplest case the foliage-leaves are of small size, but still carry on assimilation, as for instance in Conifers (*e.g.* Scotch Fir, Fig. 145, Arbor-vitæ). Other plants show a reduction of the leaves to mere scales, more or less destitute of chlorophyll, the assimilatory functions being transferred to the stem (*e.g.* Broom).

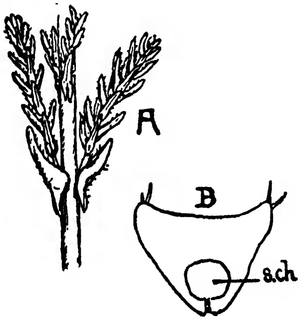

FIG. 78.—*A*, small portion of a plant of the Heather; *B*, a leaf of the same cut across to show how it is rolled up; *s.ch.*, the inner cavity thus formed which is full of water-vapour.

The transpiring surface is also reduced by restriction of the stomata to a groove or grooves or by the folding of the leaf. Examples of such *grooved or rolled leaves* are found in many heath-plants (*e.g.* Heather or Ling, Fig. 78), as well as in the Marram Grass (*Psamma*).

Other plants of dry places exhibit a modification of their leaves or branches to form hard stiff pointed structures known as *spines*. These contain large quantities of sclerenchyma (hence their tough consistency) and consequently very little transpiration takes place from their surface. The best example in the British flora is afforded by the Gorse or Furze (Fig. 79, B) in which both leaves and branches are spiny. That this habit affords protection against excessive transpiration is indicated by the fact that plants grown in a moist atmosphere (*e.g.* a damp greenhouse) produce few or no spines and develop normal flexible foliage-leaves, although of small size.

There are many other examples of spinous plants in our flora, in which the spines are not an obvious adaptation to drought (*e.g.* Gooseberry, Sloe). The true character of such spines can be determined by their position with reference to leaves or leaf-scars and the presence or absence of a bud between the spine and the stem upon which it is borne. Stem-spines are seen in the Sloe (Fig. 79, A) and Hawthorn, where they arise in the axil of a leaf, whilst leaf-spines are found in the Barberry subtending condensed shoots bearing the ordinary foliage of the plant.

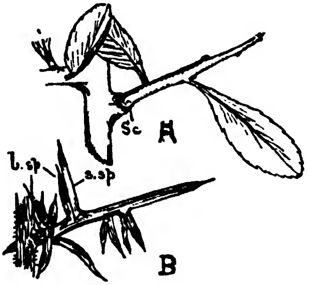

FIG. 79.—*A*, small portion of a branch of the Sloe showing a branch-spine, arising in the axil of a leaf-scar (*Sc.*) and bearing two leaves ; *B*, small portion of a branch of the Gorse showing both leaf- (*l.sp.*) and stem-spines (*s.sp.*).

All the devices for water-economy above considered effect a reduction of the amount of moisture transpired, but there is obviously a second method of providing against drought. Thus, many plants of dry places store up water in certain tissues, composed of large colourless thin-walled cells (Fig. 60, A, *a.*) and, when these represent a large part of the plant, the latter acquires a fleshy or succulent character. Such plants (*succulents*) lay up reserves of water, in times of rain, to be used during subsequent periods of drought and, as a general rule, either the leaves (*e.g.* Stonecrop) or the stem are employed for this purpose; in the latter case the leaves themselves are usually reduced to spines (*e.g.* Cactus).

The modifications of the shoot discussed in the preceding pages serve to harmonise the plant with its surroundings; so that a comparison of different kinds of plants growing under similar conditions, even in widely separated regions of the earth, will reveal much in common (*e.g.* the plants growing in loose sand). On the other hand, different surroundings entail a difference in habit, so that for example the Buttercup of the meadow differs essentially from that of the pond or ditch. Though some of these modifications vary with the conditions under which the plant grows (cf. p. 322), others are more or less fixed and tend to put a limit to the variety of circumstances under which the plants possessing them can thrive.

CHAPTER XVII

THE NUTRITIVE PROCESS OF THE PLANT

THE water which is absorbed by the roots contains various mineral salts in solution (cf. p. 9) which help in one way or another to build up the body of the plant. Although a large part is evaporated some of the water is retained, and this is employed for diverse purposes, viz. (i) in combination with the carbon dioxide of the air to form the starting-point of the organic substance of the plant, (ii) to keep the cells in a turgid condition (cf. pp. 64 and 155), (iii) to serve as a medium for transference of soluble materials from one part to another, and (iv) to permeate the cell-walls and protoplasm. Uncombined water thus constitutes a great part of the plant's body, as can be readily seen by comparing the weight of a fresh and a dried plant.

To ensure a more accurate comparison a considerable quantity (*e.g.* about 100 grams) of fresh material is cut up into small pieces, put into an evaporating dish of known weight, and the two weighed together. The dish now is placed in a drying oven and maintained at constant temperature for at least twenty-four hours. After cooling it is reweighed, the weight is noted, and then the dish is again heated; this is repeated until two successive estimations give the same result. The weight of the evaporating dish having been subtracted in each case, it will be found that the final weight of the material is far less than the original one. Since the temperature of the drying oven would be only sufficient to drive off the uncombined water, the loss of weight recorded corresponds to the amount of the latter; the weight of the remaining substance is consequently known as the ***dry weight***, and is usually expressed in percentages of the fresh weight.

The dry weight varies considerably according to the kind of plant or the portion of it used; thus, in a woody plant it amounts to about 50 per cent., in an herbaceous plant to about 30 per cent., and in a water-plant (as well as in many edible fruits) to little more than 5 per cent. We therefore see that, in all but woody plants, the uncombined water constitutes the major part of the plant's substance. This does not, however, apply to dormant seeds in which the dry weight usually represents about seven-eights of the total, and we can consequently understand why, as a preliminary to germination, so large an amount of moisture has to be absorbed (cf. p. 22).

In order to study further the composition of the plant we place the dried material, obtained as before, in a weighed crucible and heat it strongly for several hours over a Bunsen burner. The mass first becomes charred (but the temperature should not be so high as to cause it to glow) and then gradually assumes a greyish-white colour like that of tobacco-ash. During this heating process all the Carbon, Hydrogen, Oxygen, and Nitrogen compounds composing the plant are broken down and escape, chiefly in the form of various simple gases (*e.g.* carbon dioxide, water-vapour, free nitrogen, etc.), and the matter that remains (the so-called ***ash***) consists of the mineral constituents of the plant (*e.g.* silica, potassium carbonate, etc.).

If, after cooling, the weight of the ash is ascertained, it will be found to represent but a small fraction of the original dry weight (*e.g.* about 4 per cent. in a Potato, about 7 per cent. in the Clover, and as much as 17 per cent. in Tobacco-leaves). In order to obtain a fairly accurate estimate of the ash the heating must be repeated, as in the case of the dry-weight determination, until no further decrease takes place. Analyses of the ash obtained from a large number of plants has shown that it always contains compounds of the following elements, though varying considerably in their relative amounts: Aluminium, Calcium, Chlorine, Iron, Magnesium, Phosphorus, Potassium, Silicon, Sodium, Sulphur. To these we must add the elements Carbon, Hydrogen, Nitrogen and Oxygen, which were present in the dried material before its conversion into ash, so that compounds of fourteen chemical elements are practically always to be found in the plant. Not all of these are, however, really essential, as can be shown by growing plants in so-called ***water-cultures***.

These are solutions containing a mixture of various mineral salts in small quantities, so that a larger or smaller number of chemical elements may be present. A solution containing potassium nitrate, magnesium sulphate, calcium sulphate, and ferric phosphate dissolved in distilled or tap water is found to suffice for the healthy growth of many plants, if their roots be allowed to dip into the liquid. But, by eliminating one or other chemical element, the great decrease in vigour of the plants employed demonstrates that, for healthy growth, all those contained in the above solution are necessary. Thus, if Nitrogen be absent (which can be effected by substituting potassium sulphate for potassium nitrate in the culture-solution mentioned above), plants fail to reach any considerable size and sooner or later die. This shows that the great volume of free Nitrogen in the atmosphere cannot be used directly by the ordinary plant (regarding the exceptional behaviour of members of the Pea-family, see p. 255).

The experiments with water-cultures have thus proved that the following nine elements are essential for the nourishment of the plant: Calcium, Hydrogen, Iron, Magnesium, Nitrogen, Oxygen, Phosphorus, Potassium and Sulphur; to these we must add Carbon, which was proved to be necessary in the first chapter (p. 11). All of these, with the exception of Carbon, are obtained from the soil in the form of simple soluble inorganic compounds like those used to make up the culture-solutions. Some of the minerals in the soil are, however, only slightly soluble in water, but the carbon dioxide given off from the surface of the root-hairs in respiration (p. 12) unites with the soil water to form carbonic acid; this has considerable solvent powers, and thus the plant itself brings into solution some of the compounds which it requires. A striking feature of the absorptive process is that different kinds of plants growing side by side in the same soil may take up very diverse amounts of the same compound (cf. p. 70). That the process is not a simple one is shown by the phenomenon of antagonism (cf. p. 69).

The necessity for the supply of Carbon, Hydrogen, Oxygen, Nitrogen, Sulphur, and Phosphorus to the plant is obvious when the composition of protoplasm is recalled (cf. p. 57). Calcium and Potassium appear to play some important part in the building up of the latter, although they need not necessarily enter into its final composition. Chlorophyll is not formed in the absence of Iron (cf. p. 171), while Magnesium is a constituent of this substance.

It is impossible to replace the carbon dioxide of the atmosphere by any addition of Carbon-compounds (*e.g.* carbonates) to a water-culture solution or to the soil-water. Carbon dioxide, which is thus indispensable to the formation of carbohydrates in green leaves, is found only in small amount in the atmosphere (about three parts in 10,000 of air) and obtains access through the stomata (p. 129). For, if the under-sides of the leaves of a *Fuchsia*-plant be covered with vaseline, the shoot having previously been kept in the dark until all the starch has disappeared, none will be formed on exposure to light. On the other hand, a control-plant with unvaselined leaves, but otherwise similarly treated, gives the starch-reaction after a short time. The carbon dioxide, diffusing through the intercellular spaces between the cells of the mesophyll, ultimately reaches the chloroplasts, where the actual process of CO_2-assimilation takes place.

An experiment was described in the first chapter (p. 10) illustrating the importance of *chlorophyll* in carbon dioxide assimilation, a fact that can also be proved by applying the iodine-test to variegated leaves (*e.g.* variegated Privet).

If a chlorophyll-solution[1] is obtained in the way described on p. 10, it will be seen to have a deep green colour when held up to the light, but when held against a black background, so that the light is reflected from it, the solution appears a dark reddish-green. It will be a familiar fact that daylight is a combination of rays of all colours, and our previous observation shows that the red rays are absorbed (hence the reddish tinge in reflected light), whilst the others give the characteristic chlorophyll-colour when viewed in transmitted light. This may be verified by examining daylight, or other white light, that has passed through a chlorophyll-solution, with the aid of a spectroscope, when a dark absorption-band will be readily recognised in the red zone; other absorption-bands (in the orange and yellow zones) are also present, but these are smaller and more difficult to see, whilst a large part of the blue and violet zones is obliterated.

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[1] Regarding the chemical composition of chlorophyll, see p. 138.

In the absence of Iron- or Magnesium-compounds in the nutritive solution chlorophyll is not formed, and the plants assume a pale, anæmic appearance. If such compounds are subsequently supplied, the normal green colour is restored, just as salts of iron stimulate the production of the chemically similar hæmoglobin in human beings suffering from anæmia. An absence of green colour has likewise been noted (p. 10) in plants grown in the dark.[1]

Apart from these two essentials for chlorophyll-formation, a suitable temperature is also necessary, the pale colour of the shoots of many plants that commence to grow early in spring being a result of imperfect production of the green matter. Finally, attention may be drawn to the fact that intense light tends to decompose chlorophyll; thus, if two test-tubes containing a solution of it are kept, the one in strong light, the other in darkness, the former will soon lose its fresh green colour (in contrast to the latter) and become a dirty brown.

Fig. 80.—Starch-print. The leaf shown has been covered with a stencil-plate bearing the letter G, exposed for some hours to sunlight, then decolourised and placed in iodine-solution.

The light absorbed by chlorophyll furnishes the energy necessary for the manufacture of carbohydrates, although its rôle is evidently very complex. The necessity of light for starch-formation in the leaves of an entire plant was demonstrated by the experiment described on p. 10, and a modification of the same method is applicable to individual leaves. Thus, if a leaf is covered with a stencil-plate and placed in the light, subsequent treatment with iodine will give a dark letter on a light ground (cf. Fig. 80).

It is known that starch is not really the first substance formed

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[1] Such an absence of chlorophyll through growth in the dark is exhibited by the leaf-stalks of cultivated Celery and Sea Kale.

gas consists mainly of Oxygen. If at the same time a similar apparatus is fitted up, except that water which has been boiled (and subsequently cooled) is employed, no liberation of Oxygen will be observed, even in strong light. This is because in boiling all the carbon dioxide dissolved in the water was driven off, thus rendering assimilation impossible. The experiment also shows us that aquatic plants depend on the carbon dioxide dissolved in the water for their assimilatory process, a fact which is also apparent if we apply the iodine-test to the leaves of such a plant kept in boiled water.

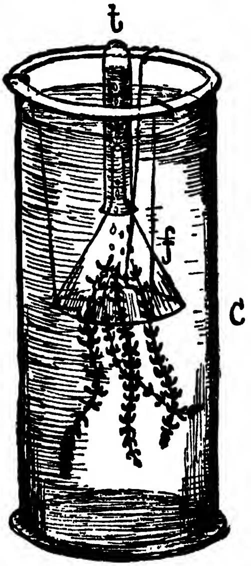

Fig. 81.—Apparatus to demonstrate that an assimilating water-plant gives off Oxygen. For description, see text.

A modification of the above experiment enables us to investigate the influence of different conditions on the process of photosynthesis. For this purpose we use a single shoot of some water-plant, the cut end of which is covered with shellac varnish in which, on setting, a small hole is pricked. The shoot is loosely tied to a long glass rod, with the cut end upwards, and placed in a cylinder of water. In bright sunlight bubbles arise from the cut surface at a considerable rate, but their number is much diminished when the cylinder is placed in the shade and still more so in a poorly illuminated room, whilst in the dark there are practically none. We thus see that, other things being equal, the rate of assimilation (as measured, for instance, by the number of bubbles per minute) decreases with the intensity of the light. The same method shows that it also diminishes as the temperature of the water is lowered and almost ceases when several lumps of ice are added. A siphon of soda-water enables us to increase the amount of carbon dioxide present in solution, and we can thus prove that the greater the amount of this gas available the more rapid is the assimilatory process.

Our discussion of photosynthesis has shown how water from the soil and carbon dioxide from the air are converted, with the help of the chlorophyll under suitable light- and temperature-conditions, into carbohydrate food-substances whose further fate must now be considered. Part of the carbohydrates, together with nitrates, sulphates, and phosphates brought up in solution in the soil-water, are built up into the still more complex proteins containing, apart from Carbon, Hydrogen, and Oxygen, the elements Nitrogen, Sulphur, and frequently also Phosphorus, and, as we have already seen (p. 169), the Calcium and Potassium salts play some part in their formation. From these proteins the protoplasm is replenished.

The carbohydrates which do not undergo these changes are in part modified to form the *cellulose*, of which cell-walls are largely composed, whilst the remainder are transferred from the leaf to other organs, where they are either used directly for growth or become stored up as a reserve. Carbohydrates are continually being thus conducted away from the seat of their formation, but on a bright day they are produced in photosynthesis more rapidly than they can be removed and consequently, towards the end of the day, many leaves exhibit an accumulation of starch which, however, disappears again overnight (cf. p. 91). This transference of carbohydrates can be readily demonstrated in any plant, whose leaves form plentiful starch, by comparing the amount of the latter in a leaf removed at sunset and in one picked early the following morning. On the other hand, detached leaves with their petioles in water do not lose their starch during the night, since it cannot be removed. Proteins, which are probably in large part built up in the leaves, since it is here that the materials for their production are chiefly found, are probably conveyed by the sieve-tubes. If, for instance, a stem of the Vegetable Marrow be dipped into boiling water so as to coagulate the contents of the sieve-tubes, the abundant proteins can be demonstrated by heating longitudinal sections with Millon's reagent. In all cases the elaborated material is transferred mainly in solution.

During the numerous chemical changes that lead up to the formation of proteins and protoplasm a large number of other substances are formed, many examples of which were considered on pp. 105–110; analogous compounds, moreover, are produced in the breaking down processes which are constantly taking place in the plant (cf. Chapter XIX).

Some plants, in which the leaves are always of small size and frequently devoid of chlorophyll, are only able to thrive when a part or the whole of their nourishment is supplied in an organic form. When such food is obtained from some other living organism the plant is known as a *parasite* and the organism on which it feeds as the *host*, while when the source of nourishment is dead organic matter we speak of a *saprophyte*.

Among British flowering plants we may select the Dodder (*Cuscuta*) as a typical instance of a parasite. This plant is an annual attacking many different hosts (*e.g.* Clover, Furze, Heather, etc.), which it entwines with its thread-like stem (Fig. 82). Some of the coils are close together and bear the suckers, or haustoria (*S*), through which nourishment is absorbed, whilst others are more distant and unattached. The haustoria penetrate the cortex and ultimately reach the vascular tissue of the host, connection being established both with the xylem and phloem of the latter. At first sight there appear to be no leaves, but careful examination discloses a number of minute scales (*l*) separated by long internodes and, as in all true parasites, completely devoid of chlorophyll. The stems vary in colour between bright yellow and red, and thus the plant becomes conspicuous, even before the rosette-like bunches of pink flowers (Fig. 82, *fl.*) are formed. The Dodder agrees with all parasites in its extensive production of seeds, so that from a single parent-plant a large quantity of offspring will arise. In this way the risk of a host not being found is minimised, since one or other of the numerous seeds is very likely to germinate near a suitable plant. The seedling is capable of a brief independent existence, but failing the presence of a host it soon dies away.

The parasite being relieved of those functions which necessitate elaboration of the vegetative structure, is enabled to utilise almost its entire energies for the purpose of reproduction. Simplification of structure, in every other direction but that which tends towards an increase in the output of seeds, is a marked characteristic of these organisms, and similar reduction combined with great reproductive efficiency characterise parasitic organisms (*e.g.* Tape Worm) among animals.

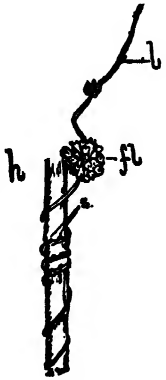

FIG. 82.—Small part of a plant of the Dodder (*Cuscuta*), showing the method of entwining the stem of the host (slightly enlarged). *fl*, flowers ; *h*, stem of host ; *l*, leaf ; *S*, suckers.

Nearly all other British parasites are so-called root-parasites—that is to say, they fix themselves by means of haustoria to the roots of the attacked plant, with which there is no evident connection overground. This is the case in the Toothwort and the Broomrapes.

The Mistletoe is only a partial parasite found growing on the branches of Apple, Hawthorn, etc. It possesses green leaves, and sends its peg-like suckers (whose growth in length keeps pace with the increase in thickness of the branch) deep down into the wood of the host. It differs from most other British plants in growing aloft on the branches of trees.

The commonest saprophyte amongst British flowering plants is the Bird's-nest Orchid (*Neottia*) found growing in the humus of Beech-woods. This plant blooms in late May, the shoot emerging from the humus as an unbranched stem bearing a few scaly leaves of moderate size and numerous flowers, all of a brown colour, little or no chlorophyll being present. The erect shoots are borne on a subterranean portion, the numerous branches of which are interwoven so as to form a structure somewhat resembling a bird's nest; hence the common name. Such a saprophyte obtains its nourishment from the organic matter in the humus (in which it is aided by a mycorrhiza, cf. p. 118) and can consequently only thrive in places where there is a plentiful accumulation of the latter.[1]

FIG. 83.—Photograph of two plants of the Great English Sundew (*Drosera anglica*). On one of the leaves of the left-hand plant an insect (*ins.*) has been caught. *bl.*, leaf-blade; *infl.*, inflorescence; *p.*, petiole. [Photo E. J. S.]

A further method of nutrition is exemplified by the Sundew (*Drosera*; Fig. 83) which frequents boggy situations, such as damp moorlands and peaty heaths. The plant consists of a rosette of reddish leaves which are provided with relatively long

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[1] Fungal parasites and saprophytes are described in Chapter XXIII.

petioles (*p*), expanding into a blade (*bl.*) which is rounded or oval according to the species; from the centre of the rosette arise one or more upright inflorescences (*infl.*) with white flowers. The upper surfaces and the edges of all the leaf-blades are beset with numerous hair-like outgrowths or tentacles having swollen ends which glisten owing to a sticky covering (see Fig. 83). Insects attracted by the latter alight on the leaf and adhere to the secretion upon the ends of the tentacles. If the insect be powerful enough, it may in its struggles manage to escape, but unless this happens at once the tentacles bearing the insect begin to bend slowly towards the middle of the blade, and this is soon followed by a similar movement of the others.

In this way the insect's body is firmly held against the surface of the leaf, in fact it is often completely hidden from view by the incurved tentacles. At this stage digestive juices pass out from these structures and, attacking the insect's body, slowly convert its soft parts into a soluble form suitable for absorption by the plant. After a considerable lapse of time the tentacles resume their normal position and now the undigested hard portions of the insect alone remain. The Sundew is able to live without such insect-food, but under these circumstances it produces fewer flowers and seeds—in other words, its vigour is much diminished.

Mention should also be made of the well-known Pitcher-plant (*Nepenthes*), in which the blade is modified to form the pitcher, the rigid lid serving to protect the contents from being flooded by rain. Insects which venture on to the slippery inner surface of the pitcher fall into the liquid, which occupies the lower part and are prevented from crawling out by the numerous downwardly directed scales upon the wall; subsequently after their bodies have been disintegrated the soluble products are absorbed by the plant.

Most insectivorous plants frequent swampy localities, and it is probable that by their special methods of nutrition they make up for some deficiency of necessary mineral salts in the water which they absorb. In such plants the customary relation of plant and animal is reversed, the latter providing a source of food for the former.

CHAPTER XVIII

FOOD-STORAGE. ENZYMES

IT has been noticed (p. 91) that during the active season all perennials produce a surplus of food which is stored up for future use in the perennating parts. In trees and shrubs these are constituted by the woody branches (cf. p. 18), but in herbs it is the underground organs which serve this purpose and which often assume special forms.

In many cases a portion of the stem persists beneath the surface of the soil, such underground stems being termed *rhizomes.* In the Solomon's Seal, for instance, the aerial flowering shoots will be found to arise vertically from a thick white rhizome (Fig. 84), situated at some depth in the soil and covered with ring-like remnants of scale-leaves[1] (*s*), as well as with roots (*a.r.*) which occur principally upon the under side. Examination of an entire plant in spring shows that the ends of the main axis of the rhizome and its branches curve up to form the overground shoots (*a.s.*), whilst a bud, from the axil of the lowest scale-leaf on the latter, continues the horizontal growth of each branch of the subterranean system.

Some time after flowering the aerial shoots die away leaving on the upper surface of the rhizome a large round scar (*sc.*), the so-called "seal," marked by numerous dots which represent the broken ends of the vascular strands. The rhizome persists for some time, so that several seals marking the annual flowering shoots may be found along its length, but sooner or later the older parts decay, and as a consequence the branches become separate plants. Owing to large quantities of food-reserves stored up in the thick underground portion, the aerial shoots are

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[1] *i.e.* small undifferentiated structures devoid of chlorophyll, cf. bud-scales.

able to grow rapidly in the spring, and the detached daughter-rhizomes are well equipped for an independent existence.

Corms, such as those of the *Crocus*, are comparable to rhizomes in which the annual segments only persist for one season, so that they are relatively short and correspondingly swollen. They bear brown scale-leaves in whose axils are the buds which give rise to the flowering shoots, the latter growing at the expense of the food contained in the corm.

Bulbs, such as those of the Tulip, Onion, or Hyacinth, consist of a number of fleshy scale-leaves (Fig. 85, A, *fl.sc.*) encircling one another and the central bud (*f.a.*), the whole arising from a flat disc-like stem (*st.*) and surrounded by a thin brown papery investment (*i*) composed of one or more scaly leaves. In a halved Tulip-bulb we can recognise in the central bud the parts of the future flower and a number of young foliage-leaves, whilst just within the flattened base are seen the rudiments of numerous roots (*a.r.*) appearing as small lines at right angles to the surface. In the axils of one or more of the fleshy scales will be found minute buds (*d.b.*), which will give rise to the new bulbs for the following season's growth. When the bulb begins to sprout, the roots exhibit a rapid growth (Fig. 85, B, *a.r.*) and, after they have become well established in the soil, the central bud elongates carrying up the foliage-leaves and the

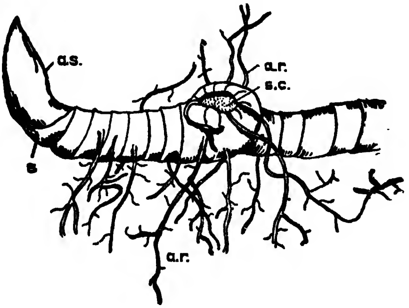

FIG. 84.—Rhizome of the Solomon's Seal in autumn (about half the natural size). *a.r.*, roots; *a.s.*, bud of next year's aerial shoot; *s.*, scale-leaves on rhizome; *sc.*, scar of aerial shoot of past season. The portion of the rhizome to the right of this scar was formed a year earlier than the part to the left of it.

terminal flower which soon expands. This growth takes place at the expense of the food-substances stored up in the bulb-scales which consequently commence to shrink (cf. Fig. 85, B).

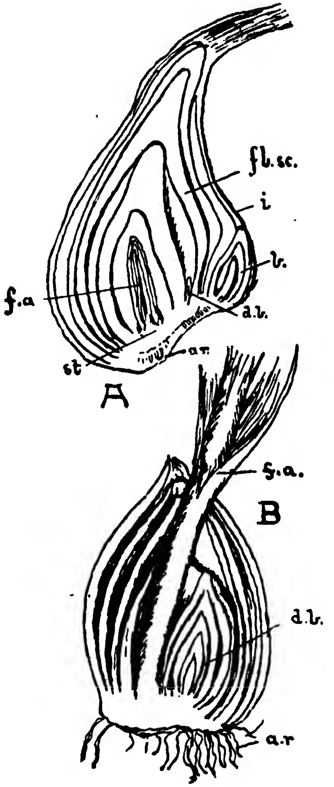

FIG. 85.—Structure and development of bulb of Tulip (natural size). A, Winter-condition in longitudinal section. B, Spring-condition in longitudinal section, only the base of the flowering axis being shown *a.r.*, roots ; *b*, incompletely developed daughter-bulb ; *d.b.*, bud which will give rise to a daughter-bulb ; *f.a.*, flowering axis ; *fl.sc.*, fleshy scales of bulb ; *i*, investment of dry scales ; *st.*, flattened stem.

It will be realised that bulbs are really nothing more than huge buds in which most of the bud-scales are swollen with stores of food-material.

Food-storage is thus in most cases associated with vegetative propagation. For example, by the rotting away of the older parts of a rhizome, the newly formed branches become separate plants. Similarly, one Tulip-bulb is generally replaced by several in the next season. This dual purpose is well seen in the Potato, where the tubers are the swollen ends of underground shoots and bear miniature buds (the " eyes "), one or more of which can give rise to a new plant at the expense of the reserves in the tuber. Many plants, however, carry on vegetative propagation without food-storage (*e.g.* Strawberry).

When a seed of the Bean or Pea germinates or a Potato sprouts, the abundant reserve-starch gets slowly converted into soluble sugars which form the starting-point from which the more complex substances required for growth are built up (cf. p. 174). A similar change takes place in the foliage-leaves at night, when the starch which has accumulated during the day is converted into sugars and removed from the scene of its formation (cf. p. 91). It is obvious that some agency must be at work in bringing about these changes, since a " starch-solution " becomes converted into sugar at so slow a rate that it is almost negligible. On the other hand, by boiling, subsequent to the addition of a few drops of hydrochloric acid, the change into sugar is much accelerated (cf. p. 97); so that after some hours the solution no longer gives the characteristic blue colour with iodine, whereas a sample of it will show the grape sugar reaction.

In the plant it is not an acid which brings about the change, but a body of the class known as *enzymes*, the one concerned in the conversion of starch into sugar being known as *diastase*. This is formed in considerable quantity at the onset of germination in all starchy seeds, and is readily obtained, for instance, from germinating Barley (the malt of breweries).[1] If some malt be ground to a fine powder (best done with the aid of a coffee-mill) and then shaken up thoroughly with water, a solution of the diastase is obtained. To eliminate other dissolved sub-

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[1] The malt is obtained by allowing moistened Barley to germinate at a moderate temperature, after which the latter is raised so as to kill off the Barley, the conversion of starch into sugar continuing owing to the presence of diastase.

stances about a pint of methylated spirits is slowly added to a small amount (*e.g.* a fluid ounce) of the filtered solution; as a result the diastase is slowly deposited as an opalescent and flocculent precipitate. The clear solution above is subsequently poured away, and the precipitate filtered off from the remainder. On redissolving the precipitate in water a moderately pure solution of diastase is obtained, a small quantity of which will rapidly convert a starch-solution into sugar. Diastase is not confined to germinating seeds, but is responsible for the change from starch to sugar wherever it is effected in the plant.

A very large number of enzymes are now known, and others are continually being discovered, but only a few can be mentioned here. The following table gives an epitome of some of the principal enzymes found in plants:

Enzyme.	Substance acted upon.	Products.
Diastase (cf. p. 97).	Starch.	Dextrin and Maltose.
Maltase (cf. p. 98).	Maltose.	Glucose.
Invertase (cf. p. 97).	Cane-sugar.	Glucose and Fructose.
Inulase (cf. p. 97).	Inulin.	Fructose.
Cytase.	Reserve-cellulose.	Mannose and Galactose.
Emulsin, Myrosin, etc. (cf. p. 99).	Glucosides.	Glucose, etc.
Lipases (cf. p. 100).	Oils.	Glycerine and Fatty Acids.
Proteases (proteolytic enzymes) (cf. p. 103).	Proteins.	Peptones and Amino-acids.
Zymase (in Yeast, p. 246).	Monosaccharides.	Alcohol and Carbon Dioxide.

The method of extraction of diastase described above is applicable to many enzymes. The material should always be ground to a fine powder, from which an extract is made usually with cold water; if the filtered solution is at all bulky, it will be convenient to reduce its volume by evaporation at a temperature not exceeding 50° C. The solution is treated with an excess of alcohol and the resulting precipitate allowed to settle. It is then filtered off, redissolved in distilled water, and can be purified by a further precipitation with alcohol.

A solution of invertase which will invert cane-sugar is readily obtained, according to Plimmer,[1] in the following manner. A quantity (100 grams) of ordinary Yeast is ground up with about 6 grams of calcium carbonate. The resulting paste is treated

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[1] *Practical Organic and Biochemistry*, p. 399.

with 5 c.c. of chloroform or ether (to kill the Yeast cells), and allowed to stand exposed to the air for three or four days, after which the enzyme is precipitated from the filtrate with an equal volume of alcohol. An impure solution of invertase, which will demonstrate the inversion of cane-sugar, can, however, be obtained by simply mashing Yeast in water with the addition of a little ether, and filtering off the solid matter (preferably through an asbestos filter).

Lipase can be prepared from the seeds of the Castor Oil by cutting up the endosperm into small pieces, and soaking these for a short time in a small quantity of ether in order to remove the oil. The material is then ground into a pulp with a very dilute (0·5 per cent.) solution of acetic acid, which sets free the enzyme. The insoluble matter is filtered off, washed till the filtrate gives no acid reaction, and the residue is shaken up with a small amount of water. If some of this suspension be added to a little olive oil, an acid reaction will soon be obtained due to the formation of fatty acids consequent upon the decomposition of the oil (cf. p. 100).

The preparation of proteolytic enzymes from plant-material is a matter of some difficulty and beyond the scope of this book. The action of such ferments is, however, well illustrated by the use of peptonising powders (containing the enzyme pepsin) to render milk more digestible for invalids.

The action of enzymes is very often a hydrolytic one, that is to say, the compound is broken down with the addition of water, thus:

$$\underset{\text{Cane-sugar.}}{C_{12}H_{22}O_{11}} + \underset{\text{Water.}}{H_2O} = \underset{\text{Glucose.}}{C_6H_{12}O_6} + \underset{\text{Fructose.}}{C_6H_{12}O_6}$$ [1]

$$\underset{\text{Inulin.}}{(C_6H_{10}O_5)_n} + \underset{\text{Water.}}{nH_2O} = \underset{\text{Fructose}}{nC_6H_{12}O_6}$$

In other cases, however, the action appears to be different, as, for instance, that of the fermenting enzymes (cf. p. 246) and of the oxidising enzymes or *oxidases* which are in part responsible for the change in colour of the cut surface of an Apple, and of

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[1] Although the formulæ for glucose and fructose are the same, these two compounds differ in the arrangement of the atoms within their molecules.

many Fungi, when exposed to air. Evidence is accumulating in support of the view that all the chemical processes depending on enzyme-action are reversible, taking place in one direction or the other according to the prevailing conditions. Thus, for example, it is believed that the building up of starch from sugar and the reverse process are both dependent on the same set of enzymes. Little is known as to their chemical nature, but all are either colloids or linked with colloidal substances, and as a consequence the rate of diffusion through parchment and similar membranes is either very slow or practically nil (see p. 69).

Our knowledge of this class of substances is almost entirely confined to their mode of action. The reactions influenced by enzymes are all such as require an appreciable interval of time for their completion, so that it is possible to measure their rate under any given set of conditions. One of the most important aspects of enzyme-activity is the small quantity of the enzyme necessary to bring about a pronounced chemical change; thus invertase is stated to invert 200,000 times its weight of cane-sugar. Moreover, at the end of the reaction the enzyme appears to be unaltered both as regards amount and characteristics. In both these respects enzymes resemble the so-called *catalytic agents* employed in certain chemical processes. As examples we may mention the use of small quantities of manganese dioxide to accelerate the liberation of oxygen from chlorate of potash, and the effect of traces of colloidal (finely divided) platinum, known as platinum black, in causing the explosive combination of oxygen and hydrogen at ordinary temperatures. In either case the reaction is one that would also take place in the absence of the catalytic agent, but with this difference, that the rate would be very much slower. Similarly, there is reason to believe that most changes brought about by enzymes would also occur in their absence, but at so slow a rate as not generally to be capable of recognition. In this connection it is well to recall that much the same effect as is produced by the enzyme can often be attained by the use of other catalytic agents (*e.g.* boiling with small quantities of mineral acids).

Although the enzyme appears unaltered at the end of the reaction, it is almost certain that combination of some kind with the substances undergoing change takes place while the process is proceeding. In view of the large surface which is presented by colloids, it is very probable that this combination is a physical one (adsorption), and it is thought by many that, in the hydrolytic enzymes, for instance, the water and the compound undergoing hydrolysis are brought into intimate contact at the surface of the ultramicroscopic ferment particles.

Enzymes differ from most other catalysers in that each is usually only effective in accelerating one or few particular reactions (cf. p. 183), and they are, moreover, very sensitive to heat and light. The rate of the reaction is doubled or trebled with every rise of 10° C., but soon a temperature is reached (usually about 60° C.) at which most enzymes are destroyed. It may be added that heating which suffices to kill the protoplasm leaves ferments unharmed. Strong light destroys them very quickly, an effect for which the violet end of the spectrum appears to be mainly responsible. Many chemical compounds (*e.g.* sulphuretted hydrogen, prussic acid, chloroform, etc.) arrest enzyme-action to a more or less marked degree according to their concentration. If the products of enzyme activity are not removed, a retardation of the process is at once manifest, continued action of diastase, for example, being dependent upon the removal of the maltose. In some cases the accumulation of the products of the reaction actually exerts a poisonous effect, as, for instance, that of the alcohol produced by Yeast. Usually, however, the substances resulting from enzyme-action are removed by the plant as soon as formed.

Enzymes frequently act only in the presence of another substance, an *activator*, which is commonly a salt, acid, or alkali, although sometimes more complex. These activators differ from the enzymes in being able to diffuse through a parchment membrane, and can consequently be separated from the latter by dialysis.[1] Examples are afforded by the small quantity of acid necessary for the action of pepsin, and the necessity of the presence of certain complex phosphatic compounds for the action of the zymase of Yeast.

Just as these substances have the effect of accelerating enzyme action, so, too, it has been seen that others have a retarding

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[1] That is to say, placing the mixture of enzyme and activator in a parchment tray floating on a large vessel with water.

influence, and there is every reason to believe that either the one or the other can be produced as may be required by the living cell. The rate of the reaction depends on the amount of the enzyme present, and this latter is regulated by the cell's activity. It is clear, then, that the character and vigour of catalytic activity is subject to considerable modification, and is indeed intimately related to the momentary requirements of the organism. Moreover, mixtures of enzymes may exhibit properties which are not shared by the components separately.

CHAPTER XIX

THE BREATHING PROCESS OF THE PLANT

THE life-processes of every living organism are always associated with a chemical break-down, the outward evidence of which is an absorption of Oxygen and a giving out of carbon dioxide. We have previously (p. 12) pointed out that this respiration goes on at all times in the plant, but is masked during the daytime by the more active assimilatory process in which the gaseous exchange is reversed. As a consequence the volume of Oxygen evolved is less than that actually formed in photosynthesis, since part of it is used for breathing; similarly, the carbon dioxide produced in the latter process is not liberated, when the plant is exposed to light, owing to its being used for purposes of assimilation as soon as it is formed. Hence an evolution of carbon dioxide from a green plant can only be demonstrated in darkness.

It is probably for the most part carbohydrate-substance that is broken down in the process of respiration in plants and, taking grape sugar as an example, we can in a general way illustrate the very complex chemical changes involved by the following equation :—

$$\underset{\text{Grape sugar.}}{C_6H_{12}O_6} + \underset{\text{Oxygen.}}{6O_2} = \underset{\text{Carbon dioxide.}}{6CO_2} + \underset{\text{Water.}}{6H_2O} + \text{energy.}$$

From this it will be seen that the volume of carbon dioxide given out is equal to that of the Oxygen taken in, and that water-vapour is simultaneously produced. This evolution of water-vapour in the course of the breathing process is a familiar fact in animals, but is difficult to demonstrate in plants owing to transpiration going on at the same time.

A method of demonstrating the necessity of Oxygen for respiration and growth was described on p. 12. If we plunge a glass rod which has been dipped into lime-water into a stoppered jar in which living plants have been confined for some time in the dark (unnecessary if the plants lack chlorophyll), the lime-water rapidly turns milky, a sure indication that a considerable amount of carbon dioxide is present; in an empty control-jar no such rapid change is observed.

That plants in breathing remove a constituent of the air can be shown by placing germinating Peas in a flask which is closed with an air-tight rubber cork fitted with a glass tube bent as in Fig. 86. Suspended in the flask by a cotton thread is a small bottle (*b*) containing a concentrated solution of caustic potash, whilst the free arm of the tube dips into a tumbler of water. Or the Peas can be suspended in a small basket of wire-gauze and the bottom of the flask covered with soda-lime. In either case the carbon dioxide evolved by the Peas, in place of the Oxygen taken in, is absorbed by the potash or soda-lime, and as a consequence a reduced pressure is produced within the flask, so that a column of water rises in the tube, as shown in the figure. To avoid the effect of changes in temperature the flask as a whole can be placed in a large vessel of water.

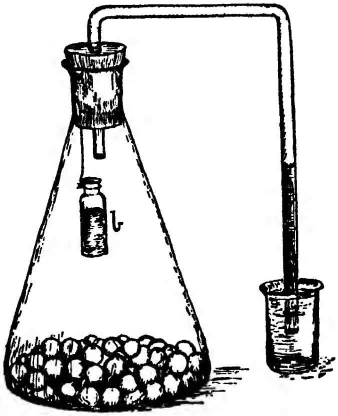

FIG. 86. — Apparatus to demonstrate that germinating Peas give off carbon dioxide in the process of respiration. For description, see text.

Since every living cell must breathe, there must be free access of Oxygen to all parts, and this is effected by a continuous system of air-spaces opening to the exterior by the stomates (p. 129) and lenticels (p. 151). If we seal up the cut end of the petiole of a detached leaf and place the whole in warm water, the bubbles which form above the stomata demonstrate their connection with the intercellular spaces. The fact that the lenticels are apertures giving access to the same system can be shown by placing woody twigs, in which the cut ends have been sealed with melted paraffin-wax, in warm water, when large bubbles of air will be seen to arise from the lenticels. If the stem of a plant is cut off just above the root and the latter immersed in hot water, bubbles of air will be given off from the cut surface for some little time, thus showing that the air-spaces of the root are likewise continuous with those of the stem.

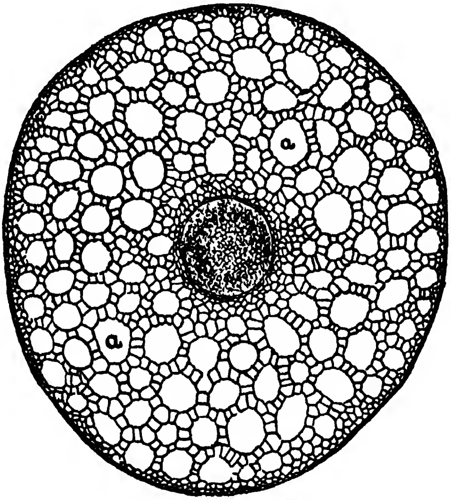

FIG. 87.—Cross-section of the stem of the Mare's-tail, a water-plant (considerably enlarged). *a*, air-spaces.

Air-spaces can be readily seen in cross-sections of the stem of any water-plant (*e.g.* the Bulrush, the Mare's-tail, Fig. 87, the flower-stalks of the Water Lily), where they are exceptionally large and serve as reservoirs for the Oxygen produced in photosynthesis. The air-system of plants serves, not only for the access of Oxygen, but also for the escape of the carbon dioxide formed in respiration and of the water-vapour which is transpired to a limited extent from all the living cells.

The quantity of carbon dioxide evolved can be determined by means of the apparatus shown in Fig. 88. The flask C containing germinating Peas is connected on either side with two wash bottles, and air is drawn through this system at a slow rate by means of an aspirator or a filter-pump. The first bottle (A) contains strong caustic soda to absorb carbon dioxide, while the second (B) contains lime-water to test the completeness of its removal. The air freed of carbon dioxide passes over the Peas, and the carbon dioxide liberated in their respiration is drawn into the third bottle (D) containing lime-water, where it is precipitated as the carbonate. The lime-water in the fourth bottle (E) ensures complete removal of the carbon dioxide. By weighing the precipitate formed in a definite time, the quantity of carbon dioxide evolved can be calculated.

Since Oxygen is essential for normal respiration, its absence usually leads to a cessation of all vital processes. This stoppage is most easily recognised in the case of growth and it has, for instance, already been shown (p. 12) that, when Oxygen is absent, seeds fail to germinate. The plant, however, unlike the ordinary animal, is not immediately killed by absence of Oxygen. When the latter is lacking in the surrounding air, plants carry on a process known as *anaerobic respiration*, during which carbon dioxide is also evolved. To demonstrate this, we first peel the coats off a number of soaked Peas, since air may be included between the testa and the cotyledons. A small test-tube is then filled with Mercury and inverted into a shallow dish containing the same substance, whereupon the Peas are passed under the mouth of the test-tube and allowed to float to the top of the Mercury. At first they are only partly visible, but gradually they become more and more exposed till, after some hours, they lie freely in a gaseous atmosphere which, displacing the Mercury, has collected at the top of the test-tube. If sufficient Peas are employed and the experiment is left for about twenty-four hours, nearly the whole test-tube will become filled with gas. This can be shown to be carbon dioxide by slipping a small piece of potash under the mouth of the test-tube when, as the carbon dioxide is absorbed, the mercury rapidly rises.

Anaerobic respiration probably represents the initial phase of aerobic respiration which is only completed if there is access of air. Carbohydrates are probably again broken down, but not as completely as in the normal breathing process, and furthermore complex substances (*e.g.* alcohols) are produced which, if they accumulate, tend to poison the living plant. If, before this has occurred, the plant is restored to a normal atmosphere containing Oxygen, it will in most cases recover and resume its ordinary life-functions.

The respiratory process of plants, like assimilation (cf. p. 174) and other functions, is markedly influenced by temperature, being slight when the latter is low and steadily increasing as it rises. The effect on respiration can be studied in the following way. To a little distilled water in a test-tube one or two drops of phenol-red are added and the whole shaken up with a little tap water.[1] A single germinating Pea is then introduced. The time taken for the solution to become yellow (owing to the action of the carbon dioxide on the indicator) is a measure of the rate of respiration of the Pea. If, with the help of a water-bath, a similar experiment be carried out at a temperature about 10° C. higher, the time requisite for the colour change will be appreciably diminished. A very slow rate of breathing is exhibited by

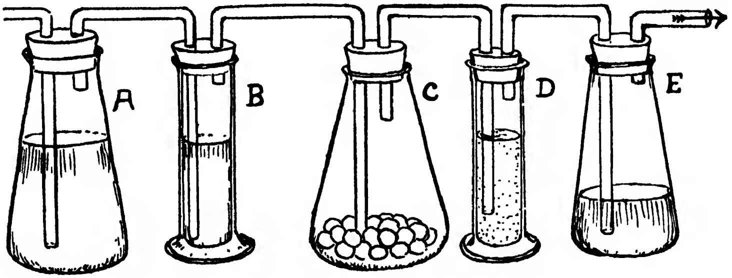

FIG. 88.—Apparatus for determining the quantity of carbon dioxide produced in respiration. Description in the text. The arrow indicates the direction in which air is drawn through the apparatus.

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[1] The phenol-red must be introduced in so small a quantity that, on blowing through a tube into a similar sample, the indicator rapidly changes its colour.

dormant structures containing little water, *e.g.* dry seeds and many Lichens and Mosses (such as grow on tree-trunks) which remain alive, even when apparently dried up.

Our consideration of respiration has shown that it entails a breaking down and loss of substance. Since under ordinary circumstances assimilation is so much in excess of respiration, this loss is scarcely noticeable, but if we prevent assimilation by placing a green plant in the dark it is easy to show a decrease of organic substance. Two lots of about five Peas (of approximately equal size in the two cases) are weighed, whereupon they are separately soaked and placed to germinate, the one lot in the dark, the other in the light. After about a fortnight the dry weight (p. 167) of both lots of seedlings is determined and compared with the weights of the original seeds,[1] when it will be found that the seedlings grown in the dark have lost considerably, while those grown in the light have gained.

The equation on p. 188 shows that the substances produced in respiration (viz. carbon dioxide and water) are the same chemically simple ones, from which the green plant builds up carbohydrates in the course of photosynthesis. It was pointed out in dealing with the latter process that a considerable amount of energy was required to accomplish this change (p. 172), and an exactly equivalent amount is of necessity again liberated, when the carbohydrates produced are broken down in the course of respiration. The setting free of energy during this process is manifest in many actively growing structures which often breathe with such vigour that a portion of the energy liberated takes the form of heat (cf. p. 248).

Thus, if a thermos flask be filled with germinating Peas or young flower-heads of the Dandelion, packed round the bulb of a thermometer, the latter will soon record a higher temperature than one in a control in which cotton-wool is substituted for the plant-material.

The energy liberated in respiration furnishes the driving power for the plant's machinery, supporting not only life itself,

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[1] It would be better to compare with the *dry weight* of the original seeds. This can be approximately estimated by determining the dry weight in percentages of the original weight for a number of Peas, and working out the dry weight of those employed in the experiment by simple proportion.

but all the vital functions as well, and we can therefore understand why the latter cease when normal respiration is arrested. In anaerobic respiration an almost negligible amount of energy is liberated, and few or no vital processes are manifested. It may be mentioned, however, that, particularly among the Bacteria which are responsible for many virulent diseases (*e.g.* Anthrax, Cholera, Typhus), there are organisms which not only ordinarily exist in the absence of Oxygen, but to whom this gas, except in minute quantities, is actually a poison. Hence the importance of ventilation in the prevention of disease.

CHAPTER XX

The Growth of the Plant

The energy produced in respiration in the members of both the Vegetable and Animal Kingdoms is utilised for such manifold purposes that a constant supply of food to provide the materials for breathing is a necessity to every living organism. The expenditure of energy by the average animal is, owing to its motile habit, very considerable and, in this respect, the animal contrasts very markedly with the ordinary terrestrial plant which, during the greater part of its life, is storing up energy in excess of its immediate requirements. It has been seen that the small quantity of energy necessary to maintain life in the ordinary plant can be supplied for some considerable time by anaerobic respiration, whereas animals perish almost immediately in the absence of Oxygen. The energy stored up by plants is usually expended in the formation of flowers and fruits at the period of reproduction. A striking example is furnished by the Talipot Palm (*Corypha umbraculifera*) which, through a period of some thirty years, carries on vegetative activities only, and then brings its life to a conclusion with the production of a stupendous display of flowers.

One way in which the energy of respiration is dissipated is in the process of growth, during which part of the food-material produced in the course of nutrition is used in building up new tissues. All growth comprises three distinct phases, viz. (i) the formation of new units by the division of the cells of the growing points (cf. pp. 7 and 73), (ii) the enlargement of the new units (p. 79), and (iii) the modification of the same to perform the different functions which they fulfil in the life of the plant (cf. Chapter VIII). Of these the second is the only phase of growth visible externally and constitutes what is known as growth in popular parlance.

The *growing points*, which are situated at the extreme tips of the shoot (Fig. 28, *g.pt.*) and just behind the root-cap (cf. p. 35), have been seen to consist of numerous small cells which during growth undergo repeated division. The restriction of growth to these definite regions is a marked feature of contrast between the growth of plants and of higher animals. A further distinction is seen in the continual formation of new organs (leaves, branches, roots) from the growing points of plants, whereas in the ordinary animal the number of organs remains constant after the embryo-stage is over.

It has been pointed out that in roots elongation is restricted to a very short portion (p. 37), whilst in stems it is spread over a much greater length (p. 197), but if we adopt means to compare the rate of increase of different parts of the elongating zone we shall find that it is not uniform. This can be done in the case of roots by repeating the experiment described on p. 36 (Fig. 16) and noting the exact amount of growth in length between each pair of marks. As we have seen, the intervals near the tip of the root will have elongated little, but, as we pass progressively farther from the apex, the intervals become wider and wider until they reach a maximum width; beyond this they again exhibit a gradual decrease till we come to the mature zone, where no growth in length has taken place (see Fig. 16, B, p. 36).

The result of this experiment can be more easily realised if a curve (graph) be constructed in the following way (Fig. 89): On a horizontal line equal divisions are marked off, equivalent in number to those upon the root, and from each mark an ordinate is raised, whose length is proportional to that of the corresponding segment on the root. By joining up the ends of the verticals (as in Fig. 89) a curve is obtained which rises to a summit and then falls again.

As we pass away from the tip of the root we come to older and older segments (*i.e.* intervals between two marks), and in the above experiment therefore we are comparing the amount of elongation in segments of different ages. This shows us that the cells of the newly formed segments elongate but slightly at first, but, as they get older, grow in length more rapidly until when they approach maturity their rate of elongation again decreases. This gradual rise and fall in the rate of elongation is spoken of as the *grand period of growth*, and, since the cells in a given transverse plane exhibit the same rate of increase, the successively older segments epitomise the changes of the individual units.

A similar grand period is exhibited by growing stems and can be well seen in seedlings. If we mark the plumule of a Runner Bean in the way previously described for the root (p. 36 and Appendix II), but over its whole length, we shall find after a day or two that the intervals have elongated over a much wider zone than in the case of the radicle; they show, however, the same gradual increase and decrease as we pass backwards from the tip. It is instructive to mark the radicle of the same seedling for the sake of comparison.

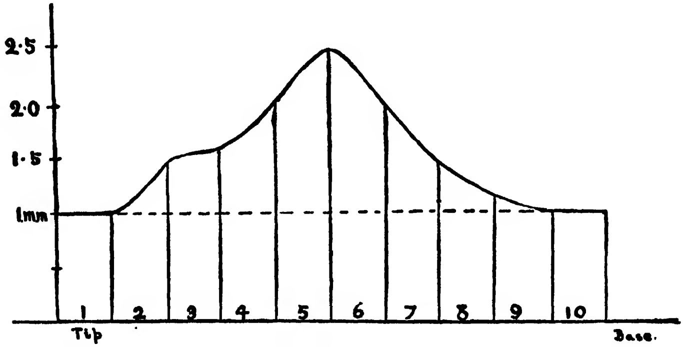

FIG. 89.—Graph illustrating grand period of growth, constructed from radicle shown in Fig. 16, B. The tip and base of the radicle are indicated.

If we require to measure the rate of growth of an entire organ we can adopt one of several methods. The simplest is, of course, direct measurement, the observations being made at regular intervals (*i.e.* daily, every two days, etc.). This is the method most easily applicable to roots which for this purpose are grown in a box with a sloping glass front. Since the rate of growth (except in such plants as Bamboos) is very slight, increased accuracy is obtained by magnifying it. For this purpose we use an instrument known as a *growth-lever* (Fig. 90) which can readily be constructed.

It is composed of a light wooden lever[1] (*l*), with two unequal arms, working on a metal pivot (*p*) which consists of a fine nail that passes through a piece of tin (*t*) doubled over the lever at this point (see the small inset in Fig. 90). A small strip of lead (*w*) (*e.g.* from the covering of a tea-packet) is wrapped round the short arm of the lever, so as nearly to balance the weight of the long one. The pointed end of the lever works over a graduated cardboard arc, the divisions of which show the actual amount of movement exhibited by the short arm. The growing tip of the plant to be experimented with is surrounded with a small pad of cotton-wool, round which one end of a thread is then firmly tied, the other end being attached to the short arm of the lever in such a way that the pointer is at the top of the scale. As the plant grows the pointer will sink and thus the amount of elongation can be noted.

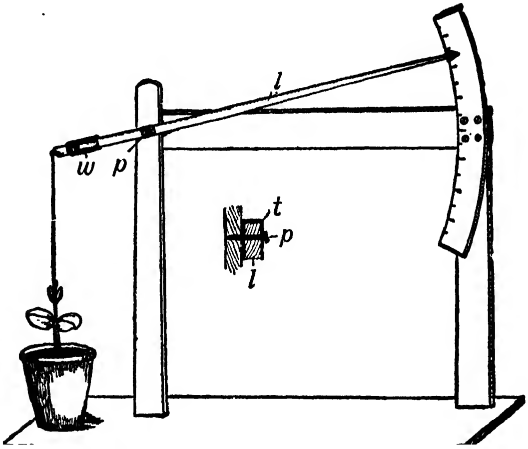

FIG. 90.—Simple form of growth-lever. For description, see text. The small figure in the middle explains the mode of attachment of the lever to the upright support.

It is sometimes convenient to measure the hourly growth of a plant, and for this purpose we require an instrument known as an *auxanometer*. Several types of the latter can be purchased

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[1] This can be made from an ordinary thin garden-stick by planing down the surface.

(see Appendix VIII), but the following instrument (Fig. 91) has certain advantages over the others and moreover is cheaper. The flat wooden base bears (i) an adjustable pillar on the top of which a light wooden lever works, (ii) an upright, to the back of which a wooden arm is pivoted about an inch from its top. The arm bears at its upper end a frame which securely holds a square piece of glass; the lateral movement of this arm is restricted by two adjustable screws. At the lower end of this arm is a projection whose end bends downwards at right angles. A cheap clock is fixed face upwards (Fig. 91) behind the movable arm in such a position that the minute-hand in its movement will come into contact with the projection. The position of the clock is such that the minute-hand, after pushing aside the arm some little way, ultimately loses contact with it, so that it swings back to its original position; this takes place automatically, owing to the glass plate being placed slightly to one side at the top of the arm. The pointed end of the lever just touches the surface of the glass plate.

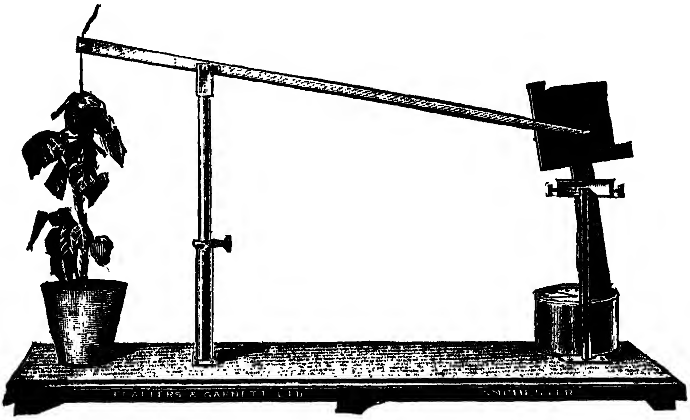

Fig. 91.—Simple form of auxanometer. Description in text.

To prepare the instrument for use, the glass plate is removed from its frame and covered with a uniform layer of soot by holding it over the smoky flame of burning camphor. The tip of the plant is attached as before by a cotton-thread to the short arm of the lever. As in the case of the growth-lever, the growth of the plant leads to a gradual fall of the pointer, which consequently traces out a vertical line on the sooted surface. Every hour, however, the glass undergoes a lateral movement, whereby the pointer is caused to make a horizontal mark, so that if the experiment be continued for some time we get a series of horizontal lines, the intervals between them representing the magnified hourly growth.

Both the growth-lever and the auxanometer will enable us to determine the conditions influencing growth. Thus, by both means we can establish that elongation is more rapid at night than during the day (provided the temperature remains approximately uniform), although the auxanometer is somewhat more helpful in this connection. The marks made by the pointer will be found to be farthest apart after midnight and nearest together after midday, whilst in between a perfect gradation connects the two extremes. This shows us that there is a *daily period* in the growth of the plant, due to the alternation of light and darkness. With the growth-lever, by taking readings in the morning and in the evening on successive days, it will also be found that the total growth at night is greater than that in the day.

The increased rate of elongation in the dark is well seen in certain plants (*e.g.* seedlings, sprouting Potato-tubers, etc.) when grown in the total absence of light. Under these conditions, apart from the non-development of chlorophyll (cf. p. 10), they exhibit an exceptional elongation of the internodes, whilst the leaves remain of small dimensions (Fig. 92, A) ; such plants are said to be *etiolated.* Even dull light has a similar effect, and many herbaceous forms (*e.g.* Willow-herbs) exhibit longer internodes in the shade of a woodland than when growing in the open. Similarly the herbs are often appreciably taller on the shady than on the sunny side of a hedge. This acceleration of growth in darkness is of great advantage in nature, especially in the case of shoots which commence their development underground (*e.g.* plumules and shoots of herbaceous perennials), since by virtue of this feature they reach the surface rapidly.

In plants whose stems grow underground the absence of light induces exceptional elongation of the petioles, a fact which is made use of in the commercial production of Celery, Rhubarb, and Sea Kale. A further interesting effect of absence of light can be observed in certain rosette-plants (*e.g.* Houseleeks, etc.) in which well-marked internodes, separating the leaves from one another, are produced under these circumstances, so that the plant acquires quite a different habit.

Apart from its influence on the rate of growth, the intensity of the light also in some cases affects the extent of development of plant-organs. Most of the buds within the crown of shade-casting trees, for instance, fail to develop, whereas at the margin the majority of them give rise to branches; and we may even find that the crown is denser on the side facing south than on that facing north. Similarly many herbaceous plants (Pig-nut, Yellow Dead-nettle, etc.) flower little, if at all, when growing in the deep shade of a wood, but do so profusely after the latter is coppiced. If the leaves of two plants of the same kind growing respectively in the sun and in the shade (*e.g.* Dog's Mercury, Enchanter's Nightshade) be compared, it will be found

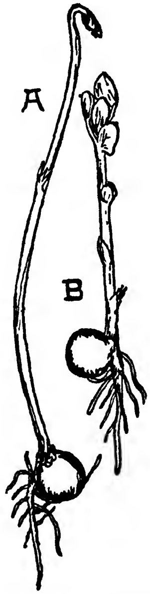

FIG. 92.—Seedlings of the Pea (about three-quarters natural size), normal (B) and etiolated (A). Both are of the same age.

that the blades of the sun-form are smaller and thicker than those of the shade-form (Fig. 93). A similar difference will be found between the exposed and shaded leaves of the same plant (*e.g.* the Beech).

In the above experiments it was stated that, in order to observe the accelerating influence of darkness, it is necessary to keep the temperature approximately constant. As can be shown with the growth-lever, this is due to the fact that heat and cold exert a profound effect on growth, as on other functions (cf. pp. 174 and 192), inasmuch as plants grow slowly at a low temperature, whilst as the latter rises the rate of elongation increases until a degree of heat is attained which is unsuitable for further existence. Since the temperature at night is usually lower than in the day, the tendency to more rapid growth at night is masked in nature.

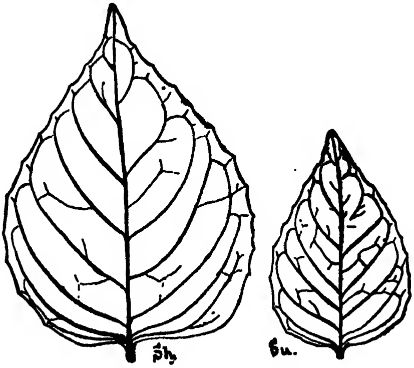

Fig. 93.—Sun- (*Su.*) and shade-leaves (*Sh.*) of the Enchanter's Nightshade (about one-half natural size).

The effects of temperature-conditions upon growth are well illustrated by several observations on plants in their natural environment. Thus, whereas some exhibit vigorous growth already in the early spring (*e.g.* Dog's Mercury, Lesser Celandine, Elm, Willow), others have to await a higher temperature and do not become active till the end of April or May (Ash, Beech, Horse Chestnut). Many plants (*e.g.* Lily of the Valley) moreover can be induced to grow and flower out of season by exposing them to a warm temperature (*i.e.* forcing them). The northward and southward extension of plants of warmer regions again is limited by the lowest temperature at which they can grow; thus, certain Palms can exist in the open in the south of England, but not farther north. But such limitation is complicated by the fact that a higher temperature and illumination are necessary for seed-production than for vegetative growth. Many tropical plants can be cultivated in a hothouse.

Apart from illumination and temperature, the most important condition influencing growth is the supply of Oxygen, but this has already been considered in the last chapter (see also p. 12). An adequate supply of moisture and nutritive material is also essential.

If we examine closely the growing apex of a shoot it will be found not to move upwards in a straight line, but to describe a slightly irregular, usually somewhat spiral, course. Such *circumnutation* is generally not apparent unless we employ special means to demonstrate it, although it is not difficult to observe in an uncurved tendril. The phenomenon (which is exhibited by stems and roots alike) is due to one side of the apex growing more rapidly than the opposite one, the zone of more rapid growth continually shifting its position round the circumference of the stem. As a result the growing tip is not straight, but exhibits a slight, often scarcely recognisable curvature, in one direction or another.

In plants the growth of one organ is often materially influenced by that of another, so that if the one is favoured or arrested, the other exhibits a reduction or promotion. We have already met with several instances of such *correlation*. Thus, in certain etiolated plants the poor development of the leaves (p. 200) is associated with greater growth of the stem. If the terminal bud is removed from a shoot, laterals which would otherwise remain dormant are caused to sprout (*e.g.* pruning; and cf. p. 46). In those forms, moreover, in which extensive vegetative propagation obtains, reproduction by seeds is generally rare, a correlation plainly shown by many cultivated bulbous plants.

The effect of an injury to any living part of the plant is to cause the surrounding cells to undergo active division, whereby the wounded surface sooner or later becomes covered up with a new growth. When a branch of a tree is removed by a clean cut, new tissue gradually develops from the margin of the exposed surface, forming a protecting rim which covers in the sapwood. A similar stimulation to growth is seen in those cases in which injury due to Insects or Fungus-pests leads to the formation of so-called *galls* (Fig. 94). In Insect-galls the special growth results from the laying of an egg or eggs by the female beneath the surface-skin and, in the same species of plant, different kinds of gall may be produced by different insects (*e.g.* Oak-apple gall, Cushion-gall, Fig. 94 C, Button-gall, Fig. 94 B, Bullet-gall, etc., all on the Oak). In some Insect-galls the high degree of mutual adaptation is illustrated by the fact that a nutritive tissue is developed around the larva of the gall-insect. The abnormal growth known as the Witch's Broom is due to various fungal pests which lead to an exceptional branching of the attacked part, examples being commonly seen on the Cherry, Birch, and Elm.

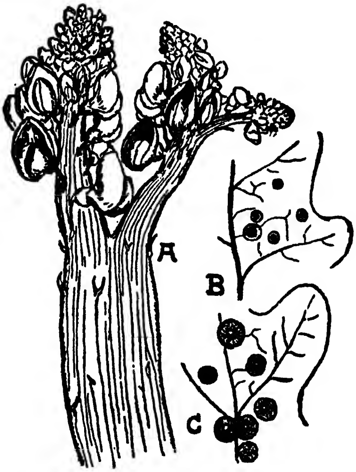

Fig. 94.—A, Abnormal specimen (monstrosity) of the Runner Bean inflorescence in which the branches have combined to form a flat axis. B, Button-gall of Oak. C, Cushion-gall of Oak. (All figures about two-thirds natural size.)

Occasionally plants exhibit unusual forms of growth which, as in similar examples in the Animal Kingdom, probably result from disturbances in the metabolism of the organism. These find expression in various ways, commonly in a combined development of the different branches of a shoot-system, so that the whole forms a flat structure (Fig. 94, A). A similar process leads to the production of the Cauliflower, an abnormal growth which has become more or less permanently fixed by cultivation.

The stimulation to growth as a result of wounding is made use of in the propagation of plants by cuttings, as well as in the processes known as *budding* and *grafting*, which are much employed in Rose- and Fruit-culture. In grafting, a portion of a twig is removed from one plant (the *scion*) and its tapered lower end is pushed into a V-shaped slit in the wood or under the bark of the stock, so that the wood and phloem of the latter are in contact with those of the scion. The cut surfaces of scion and stock, thus brought together, become intimately associated owing to fusion of the intact cells, usually accompanied by some cell-division.

Grafting and budding are usually only possible between related types of plants. The general effect of the process in the case of Fruit-trees is to bring about earlier and more abundant fruit-production. Such vegetative propagation is also advantageous as enabling florists to perpetuate forms which fail to produce seeds, or do not remain true to type (cf. p. 333).

As was mentioned at the beginning of this chapter, growth comprises the three phases of cell-division, enlargement, and cell-differentiation. It appears that the second of these phases is largely, if not entirely, dependent on the production of a diffusible substance, termed a *growth-hormone*, by the cells of the apical meristem. This diffuses to the more mature cells where it accelerates enlargement and perhaps also cell-differentiation after the manner of a catalyst. In organs which are performing growth-curvatures (p. 206), a greater amount of the hormone is detectable on the convex side, but it is still unknown how this unequal distribution is conditioned by one-sided stimulation by light or gravity.

CHAPTER XXI

PLANT-MOVEMENTS

As a result of elongation during growth the positions of the growing points are continually altering, *i.e.* they exhibit a forward movement which, as we have seen (p. 203), does not take place in a straight line. In all such cases the slight curvatures occurring during circumnutation ensue in the natural course of events and are not due to external influences or *stimuli*. One, however, frequently meets with other growth-movements leading to curvatures which can be definitely ascribed to outside agencies. The effect of the latter is to produce a change in some specially receptive portion of the plant, which ultimately results in a curvature in the zone of elongation.

Attention has already been called to the influence of gravity in inducing the upright growth of the ordinary shoot (p. 19) and the downward growth of the main root (p. 40), the phenomenon being referred to as *geotropism*. The experiments already described sufficiently illustrate these general facts, and it need only be added that an organ which curves in the direction of the force of gravity is said to be *positively*, whilst one which curves the opposite way is said to be *negatively*, geotropic.

It might be thought that the downward curvature of a horizontally placed root was due to its own weight, although the negative behaviour of the shoot makes this unlikely, as well as the absence of curvature in a dead root. Even when a certain amount of resistance has to be overcome, however, roots will nevertheless be found 'to curve downwards when placed horizontally. This may be shown by filling a shallow cup with a solution of gelatine, and, after this has solidified, fixing seedlings to corks (wedged on to the edge of the cup) in such a way that their radicles lie horizontally on the surface of the gelatine. The curving roots will be found subsequently to push their way into the latter, whereas similar seedlings which have been killed by brief immersion in boiling water remain horizontal.

So long as the shoot and root are situated with their axes parallel to the line of action of gravity, no curvature takes place, *i.e.* there is a condition of equilibrium. As soon, however, as either occupies any position other than the vertical, this state of equilibrium is upset and curvature sooner or later takes place until gravity again acts *equally on all sides.* The condition for a geotropic curvature in an ordinary shoot or root is therefore a one-sided action of gravity. If a seedling is placed horizontally in the dark and then slowly rotated on its own axis, it will of course be exposed to such one-sided influence; as a result of the rotation, however, all sides in succession will be subjected for an equal period of time to this one-sided stimulus and consequently no curvature will be observed.

To perform this experiment we use an instrument known as a *klinostat,* in which a clockwork mechanism rotates the plant at a constant slow speed (about once in twenty minutes). In carrying out experiments like that described in the preceding paragraph, control-seedlings should be laid horizontally beside the klinostat.

It will be evident that such structures as rhizomes, lateral roots, and the horizontal branches of trees respond neither positively nor negatively to gravity, but are in a position of equilibrium when more or less at right angles to its line of action. This can be shown by planting a rhizome in an inclined position, when the growing zone will be found to curve until the apex again lies horizontally.

A given organ does not always show the same response to gravity in all stages of its development. A good example is afforded by the Poppy (Fig. 95), in which the upper part of the flower-stalk is positively geotropic before the flower opens (*a*), horizontal during the process of opening (*b*), and negatively geotropic when fruit-formation begins (*c* and *d*).

If a seedling, in which plumule and radicle have been marked in the way described on p. 36, is placed horizontally in a dark box (cf. p. 40), it will be found that the curvature after twenty-four hours has in both cases taken place approximately in the region of maximum elongation. Moreover, it will be noticed that both the extreme tip and the older part of each organ have remained almost straight. Various experiments suggest that geotropic stimulation is mainly perceived by the apical region of the root. But both experimentation and interpretation of the results are beset with such difficulties that the perceptive mechanism is still obscure. There is, however, some indication that the region of curvature is farther from the apex than the region of chief perception and, if this be so, the stimulus must somehow be conveyed to the zone of curvature. Roots, from which the apical regions have been removed, usually fail to curve when placed horizontally, though, if the tips be previously reinstated with the help of melted gelatine, response to such stimulation occurs. Since, however, replacement of the tip *after* stimulation is likewise followed by a response, even though the roots be now kept vertical, it seems that the presence of the

Fig. 95.—Flower-buds, flowers, and fruit of the Poppy, showing the successive positions (*a–d*) of the flower-stalk in successive stages of development (about one-half natural size).

tip is somehow essential for curvature. Experiments suggest that in shoots also perception is mainly localised in a region separate from that which responds.

The ordinary erect shoot has been seen to respond to one-sided light by curving more or less markedly towards it (p. 19, Fig. 7, B), so that it exhibits *positive heliotropism* (*phototropism*). The tendrils of the Virginia Creeper and the rootlets of the Ivy furnish the commonest instances of *negative heliotropism*, but the majority of roots appear to be unaffected by one-sided light.

For exact experiments on heliotropism it is best to employ a dark chamber of the type shown in Fig. 96; any long wooden box (which should not be less than 2 feet in length and about 1 foot broad by 1 foot high) will serve the purpose. This is made light-tight and painted black inside to prevent reflection. A small slit-shaped piece (about quarter of an inch wide and 5 to 6 inches high) is cut out of one of the ends of the box and a piece of board nailed on either side to increase the depth of the slit (see Fig. 96); the opposite end is hinged and serves as a door for introducing and removing plants.

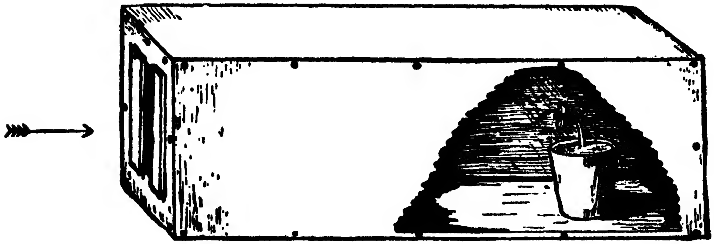

FIG. 96.—Dark chamber for experiments in heliotropism. Description in text. The arrow indicates the direction of the light.

In open spaces in nature light and gravity act together in producing the upright growth of the ordinary shoot, but at the edges of dense thickets and in hedges, where one-sided light comes into play, positive heliotropism is stronger than the negative geotropism, so that the shoots grow towards the light. With the help of the dark chamber, it can be shown that the relative effect of the two influences varies in different plants; thus, the shoots of some (*e.g.* Pea) assume an almost horizontal position, whilst others curve to a less extent (*e.g.* Cress, Runner Bean), showing that they are more strongly affected by gravity.

That erect shoots do not curve, when uniformly lighted on all sides, is shown by every-day observation, as well as by the fact that no curvature takes place when a plant is rotated on a klinostat at right angles to the source of light, since each side is then in turn equally illuminated. If we mark the plumule of a seedling at equal intervals and then expose it to one-sided light in the dark chamber, it will be found that, as in the case of geotropic curvatures, the bending ensues in the region of maximum elongation.

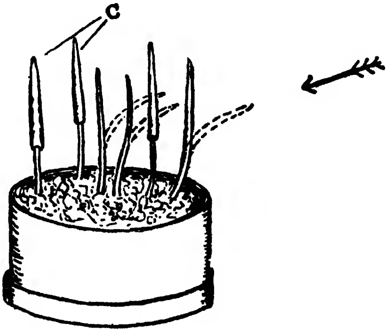

FIG. 97.—Experiment to demonstrate the localisation of light-perception in young seedlings of the Canary-grass. The arrow shows the direction of the incident light. *c*, caps of silver paper. The positions occupied by the uncovered seedlings at the end of the experiment are indicated by dotted lines.

Another analogy between the two kinds of phenomena is seen in the existence of plant-organs which respond to the influence of light by taking up a position more or less at right angles to its direction (*e.g.* dorsiventral leaves). A further similarity lies in the change from positive to negative heliotropism exhibited by the flower-stalks of the Ivy-leaved Toadflax, very common on old walls in many parts of England.

The power of perceiving one-sided light has also been shown in some cases to be localised in certain regions, a fact which can be demonstrated in young seedlings of Canary-grass in which the leaves of the plumule have not yet burst through the protective sheath. The tips of some are covered with small caps (Fig. 97, *c*), each about half an inch long and made by twisting silver paper round the point of a pin, whilst others are left uncovered. The whole pot is then placed in the dark chamber above described (Fig. 96). After about twenty-four hours the uncovered seedlings will have bent in the usual way towards the light, whilst the others have remained straight. The perceptive power is therefore in this case localised in the upper part of the plumular sheath and, as in the geotropic curvature of roots, there may be a conduction of the stimulus to the region in which bending takes place.

It has already been seen (p. 41) that an unequal distribution of moisture produces a positive growth-curvature in roots, a phenomenon known as *positive hydrotropism.* In nature, hydrotropic curvatures are rarely seen except in the case of the finer branches of the root-system, but they are of considerable value in carrying these rootlets into regions of greater moisture. We shall subsequently (p. 292) also become acquainted with growth-curvatures which are the result of a chemical stimulus.

There is obviously a certain parallel between the different bending movements so far considered, especially between geotropism and heliotropism. In both cases there are organs which respond positively, others which respond negatively, and still others which place themselves at right angles to the directive stimulus. Further, in all cases the curvature ensues in the zone of elongation, somewhere about the region of maximum growth in length, and is due to the convex side elongating more rapidly than the concave. In certain organs, moreover, the region of perception has been seen to be probably separated from the region of curvature and consequently a conduction of the impression must occur.

The previous pages also show that the same stimulus may produce a totally different effect in different cases (*e.g.* gravity causes roots to curve towards the earth, shoots to curve away), so that there is obviously no definite relation between the cause of the impression and the type of effect produced. Moreover, we have seen that in some cases a given organ responds in a different way to the same agency in various stages of its development (*e.g.* flower-stalks of Poppy and Ivy-leaved Toadflax), and the same organ may respond differently according as the stimulation is intense or weak.

Certain plant-organs, however, exhibit growth-curvatures which are a result of direct contact with some foreign body, and thus differ materially from those just discussed.

The commonest examples are furnished by *tendrils* which are either simple (*e.g.* Bryony, Fig. 98) or branched threads (*e.g.* Sweet Pea). When young, the tendrils or their branches are almost straight and constitute flexible structures composed of soft turgid tissue. At this stage their growing tips exhibit a very pronounced circumnutation (cf. p. 203) which materially increases their chances of coming into contact with a support. If this occurs, the side of the tendril opposite to that touched is stimulated to grow more rapidly, whilst that in contact with the support continues to grow at the same rate as before. This brings about a curvature of the tip of the tendril (cf. Fig. 98, A) and, as a consequence, new parts of it come into touch with the support and thus receive a fresh stimulus; moreover, the resulting curvature is not confined to the part actually in contact, but also affects adjacent parts of the tendril. In this way more and more of the growing tip becomes wound round the support, so that a firm grasp is obtained.

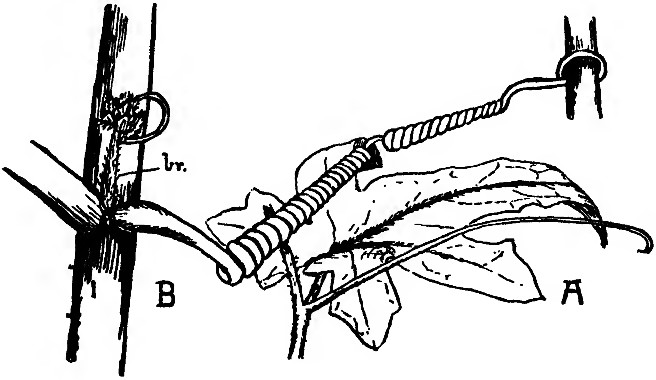

FIG. 98.—Tendrils of the White Bryony (natural size). A, before, B, after clasping the support. *br.*, branch.

After this the part of the tendril between the parent-plant and the support gradually coils up into a close spiral and, since both ends of the tendril are fixed, the coils of this spiral of necessity exhibit a reversal at some point or other (Fig. 98, B). In this way an elastic spring-like connection with the support is developed, so that the risk of the plant's being torn away by gusts of wind, etc., is diminished. Soon after its attachment the tissue of the tendril begins to thicken and harden, so that it loses its soft flexible character and becomes firm and tough. Tendrils which fail to reach a support wither away and sooner or later generally drop off.

The effect of a contact-stimulus can be imitated by gently stroking the under surface of a White Bryony tendril with the finger for about a minute. A curvature almost immediately becomes apparent and is generally very pronounced before long. As a matter of fact the changes leading to the curvature of a tendril depend, not upon the actual contact, but upon rubbing against some foreign body. This has been proved by placing tendrils in contact with a support and ensuring the absence of all vibration, when no curvature is observed. Tendrils, moreover, are not stimulated by contact with fluid bodies, so that the impact of rain-drops is without effect.

The mechanism for encircling the support in stem-twiners (p. 20) is totally different from that found in tendrils, as is readily seen by the fact that no amount of stroking of a twining stem will produce any response. It seems probable that twining in these cases is due to a peculiar action of gravity.

In many plants with compound leaves (*e.g.* Wood Sorrel, Clover) the leaflets droop down at night, recovering their normal position on exposure to light (Fig. 99). Such *sleep-movements* can also be produced by the influence of contact. Thus, if the leaflets of the Wood Sorrel be repeatedly flicked with the finger, they will after some time show a downward movement resulting in the same position as that occupied at night (Fig. 99, N). The most striking instance of such contact-irritability is that of the familiar Sensitive Plant (*Mimosa pudica*), a tropical member of the Pea-family. Here not only do the leaflets fold together in pairs, but with a sufficient stimulus the whole leaf even performs a downward movement. Moreover, after this has happened other adjacent leaves may undergo the same change, so that here again there is a transference of the original stimulus. In all of these cases the organs concerned sooner or later recover their normal position, after the effect of the stimulus has passed away.

These movements, and in fact all sleep-movements, are a result of changes in the degree of turgidity of the cells in the cushion-like, swollen base of the leaflet where the prominent cortex consists of large thin-walled parenchymatous cells. The fall of the leaflet at dusk is accompanied by a decrease in the turgidity of these cells on the lower side of the cushion, whilst at dawn they once more become turgid and lead to the elevation of the leaflet.

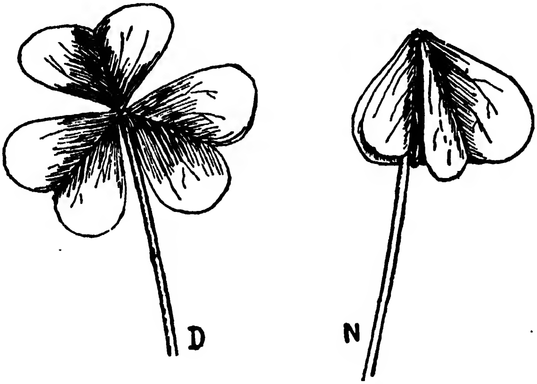

Fig. 99.—Leaves of the Wood Sorrel (natural size). D, In the day-position. N, In the night-position.

Many flowers close at night, as for example the Tulip, the Crocus, the White Water-lily, and the Wood Anemone, and these changes are quite analogous to the sleep-movements just discussed. Similarly, the flower-heads of many members of the Dandelion-family (Compositæ) close up at certain times, most commonly on the approach of night (*e.g.* Daisy), but in other cases at midday, as in the Salsify, whence the popular name for this plant "John-go-to-bed-at-noon." Night-flowering plants (*e.g.* Evening Primrose, Tobacco) have their flowers closed during the daytime, but open them at night.

The exact external cause of sleep-movements and of these

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[1] Cf. also the movements of the tentacles of the Sundew, described on p. 178.

diurnal changes on the part of flowers is only imperfectly known in most cases, but since they generally follow on the daily alternation of light and darkness, associated with which is a change of temperature, these are no doubt the two influences especially concerned. That change of temperature alone can sometimes be the determining cause of these movements is a well-known fact in the case of the Tulip, whose flowers open out widely in a warm room.

All the movements of plant-organs discussed in this chapter, like the circulation of protoplasm described on p. 59, take place only when other external conditions are suitable, the most important of these being an adequate temperature. At low temperatures the movements are either not exhibited at all or are performed very slowly. In the absence of the necessary amount of Oxygen for respiration they cease (cf. p. 191), and the same result is obtained if the atmosphere around the plant contains small quantities of anæsthetics (*e.g.* chloroform). Unless, however, these arresting influences operate for a considerable period, their paralysing effect is only temporary.

In many instances an organ exhibits a curvature, even after the stimulating cause has been for some time removed, a fact which is specially obvious in the case of geotropic and heliotropic phenomena. This is readily seen if a seedling is placed horizontally for about half an hour, its lower side being marked with Indian ink, so as to be subsequently recognisable. Before any curvature of the radicle is manifest the seedling is fixed on the klinostat, so that gravity now acts equally on all sides in succession. Nevertheless, after some little time a curvature of the radicle is observed, this taking place towards the marked side. A similar result would be obtained with a plumule exposed, for the same period, to one-sided action of gravity or light, and fixed on the klinostat before a bending movement is apparent. These experiments again demonstrate that a period elapses between the reception of the impression and the occurrence of the curvature (cf. p. 211) and further that, when a stimulus has once produced an effect, this latter cannot be obliterated by subsequent exposure to uniform conditions. Similarly, if a tendril is stroked for a short time and then left untouched, a subsequent curvature nevertheless takes place.

Plants, in common with animals, thus possess a certain power of responding to the stimuli which they receive and of adjusting themselves to their surroundings. The property of vision in animals is paralleled by the perception of light by plants, as seen in the phenomenon of heliotropism. The power of feeling is exemplified by the contact-irritability of a tendril. In these two cases, however, the animal exhibits a more highly specialised sense of perception. But where the faculty of responding to stimuli is important for the well-being of the plant, it may be even more highly developed than in animals, as is well exemplified by their respective responses to the stimulus of gravity. The sense of orientation in man, for example, is not very highly developed, since a displacement from the vertical to the extent of several degrees is absolutely unperceived by a blind-fold person, whereas a similar displacement of a plant would result after some time in a pronounced geotropic curvature.

Though they do not possess a nervous system, plants nevertheless exhibit the conduction of an impression from one part to another, a feature which is so familiar in animals. This has been seen probably to occur in geotropic and heliotropic response, and is especially striking in the case of the Sensitive Plant.

Movement of the plant-body as a whole is of less common occurrence in the Vegetable Kingdom, but is nevertheless encountered in some of the simpler plants, such as will be described in the next chapter. Moreover, even in many of the higher forms, the sexual cells (cf. p. 271) exhibit locomotion. The facts detailed in this chapter thus emphasise that movement is not a special acquisite of the Animal Kingdom, but is a property of all living organisms.

CHAPTER XXII

THE ALGÆ

PLANTS, though they exhibit a great variety of external forms, can nevertheless be collected into groups having many features, both of structure and life-history, in common. In the earlier chapters of this book the highly elaborated structure of the Flowering Plant has been almost exclusively considered, but very many vegetable organisms, of course, have no flowers and are, in fact, far simpler in every way. For example, whole groups of lower plants lack true roots and possess no vascular system, so that the Vegetable Kingdom can be conveniently divided into vascular and non-vascular plants. This difference may perhaps be related to the fact that a considerable percentage of the latter flourish in wet or damp habitats (*e.g.* Seaweeds, Mosses). The majority of non-vascular plants possess a body (*thallus*) which exhibits no definite stem and leaves.

A considerable number of the simplest types of plants consist of a single cell, and such minute organisms, by their abundance, often cause the red or green colouration of small stagnant pools. Some of the forms commonly responsible for this phenomenon belong to the genera *Sphaerella*[1] and *Chlamydomonas*, which will serve to illustrate the structure of these plants, one of whose most striking characteristics is a power of movement from place to place, usually associated with animals.

If a drop of water containing species of *Sphaerella* be examined under the microscope, the individuals will be seen to consist of an oval cell, about one-fiftieth of a millimetre in diameter. The cell is bounded by a thick wall which consists of transparent mucilage with a thin limiting membrane and which is often pro-

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[1] Also known under the names *Hæmatococcus* and *Protococcus*, although the last is altogether antiquated.

duced into a slight colourless papilla at the front end (Fig. 100, D), *i.e.* that which is foremost during movement. The mucilaginous wall is traversed by a number of, usually branched, thread-like prolongations of the protoplast extending up to the surface layer (Fig. 100, A, C). Practically the whole peripheral region of the cytoplasm is occupied by an ill-defined net-like chloroplast (Fig. 100, D, *c*), containing a number (2-8) of scattered pyrenoids (see p. 62). Near the front end of the chloroplast lies a small red speck or streak of modified cytoplasm known as the *eye-spot* (*stigma, s.*), which is believed to be concerned with the perception of light intensity (cf. below). A single nucleus (*n.*)

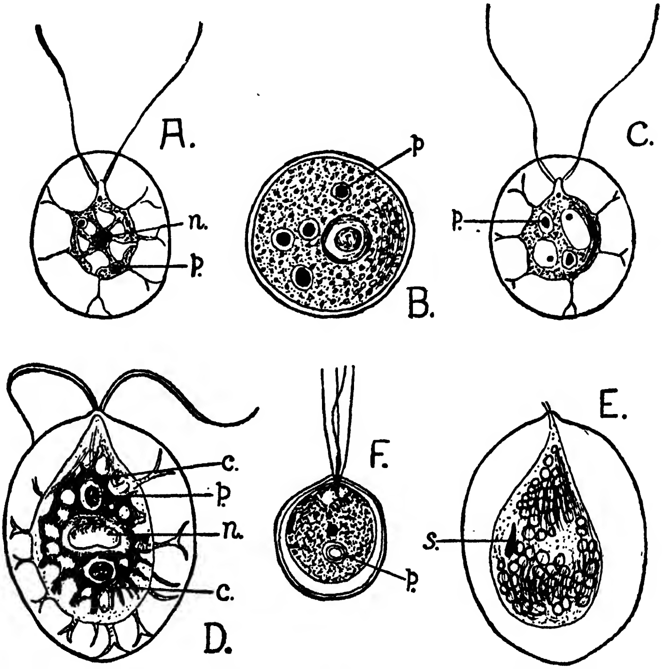

FIG. 100.—*Sphaerella* (*Hæmatococcus*). A and C, *Sphaerella pluvialis*, motile individuals (after Schmidle). B, D, and E, *S. droebakensis* (after Wollenweber). B, Resting cell; D, single individual in optical section, showing the chloroplast (*c.*); E, the same, in surface view, showing the numerous contractile vacuoles; F, an individual of *Carteria* (after Takeda). *n.*, nucleus; *p.*, pyrenoid; *s.*, eye-spot.

lies suspended by cytoplasmic strands within the centre of the cell.

If a stationary individual be observed under the high power of the microscope, small circular highly refractive vacuoles (Fig. 100, E) can be recognised in considerable numbers scattered throughout the cell, but these are much more readily seen in *Chlamydomonas*, where there are only two situated in the clear cytoplasm at the front end (Fig. 101, *c.v.*); when these are watched closely they will be seen, alternately, to enlarge gradually and then suddenly to collapse. Similar *contractile vacuoles* occur in many unicellular plants, as well as among the lower animals, and they probably serve for the excretion of waste products to the exterior.

Chlamydomonas, which is much more suitable for purposes of study than *Sphaerella*, has cells of about the same form and size. The chief points of difference are constituted by the thin cell-wall, which closely invests the protoplast, and the basin-shaped chloroplast, with usually a single pyrenoid, which occupies the back part of the cell (Fig. 101, *j*).

The movement of the individuals of *Sphaerella* and *Chlamydomonas* alike, is accomplished by means of two delicate thread-like outgrowths, the *cilia* (Fig. 100, A, C; Fig. 101, *j*), which can be detected arising close together at the front end, and are usually as long, or longer than, the body of the cell. They are recognisable under the high power in stationary individuals, but are more readily seen after adding a drop of iodine, which has the effect of killing the organisms without much change, and not only brings out the cilia, but also makes the nucleus more distinct. The cilia, as a matter of fact, are whip-like prolongations of the cytoplasm which, by their rapid backward strokes, pull the plant through the water, the movement being accompanied by a rapid rotation of the organism upon its axis. In returning to the front position, the cilia are not stretched out, and thus do not counteract the effect of the back stroke, the movements being thus comparable to those of a man's arms in swimming. The rate of travel of these organisms is very slow as measured by inches, but is rapid relative to their size.

The direction of movement is influenced by various external stimuli, such as light, distribution of chemical substances, etc.

If some water containing *Chlamydomonas* be placed in a glass bottle (covered, except for a small aperture on one side, with brown paper), after exposure to illumination for some hours, the organisms will be found to concentrate in a dense cluster

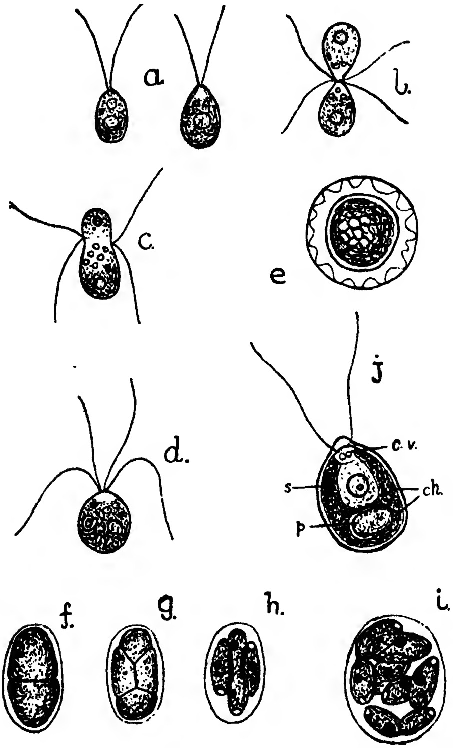

FIG. 101.—Structure and reproduction of *Chlamydomonas*. *a*, two gametes; *b*, and *c*, stages in the fusion of the same; *d*, zygote; *e*, zygospore; *f*, *g*, *h*, and *i*, stages in asexual propagation; *j*, single individual of *C. angulosa*; *ch.*, chloroplast; *c.v.*, contractile vacuoles; *p*, pyrenoid; *s*, eye-spot. (*a–e* after Goroschankin, *f–i* after Klebs; *j* after Dill.)

at the spot where the beam of light penetrates. If, however, the latter is very intense, the plants swim away from the illuminated region, which consequently becomes colourless. The influence of the direction and intensity of the light on such movements is spoken of as *phototaxis*. Just as in the case of the movements of the protoplasts within the cells of higher plants (cf. p. 59), the movement of these unicellular organisms can be temporarily arrested by slight traces of anæsthetics.

The individuals of *Chlamydomonas* and *Sphaerella*, with the help of their chloroplasts, are able to manufacture food from simple inorganic substances like any other plant, and as a result the cell grows. After attaining a certain size it comes to rest, draws in its cilia, and begins to form *daughter-individuals* (Fig. 101, *f-i*). The protoplast contracts slightly away from the wall, and, after nuclear division has taken place, gradually constricts into two equal portions, each containing half the nucleus, chloroplast, etc. The resulting segments may divide again, and these even for a third time, the successive divisions taking place in planes at right-angles to one another. Each segment develops a cell-wall and two cilia, and thus 2, 4, or 8 new individuals are constituted which, apart from size, resemble the parent in every respect.

This process of *asexual reproduction* is completed by the rupture or dissolution of the membrane of the parent-cell, with the consequent liberation of the daughter-individuals. Since, in a *Chlamydomonas*, under favourable circumstances, the succession of events just described recurs about every twenty-four hours, one individual would in the course of a week give rise to 2,097,152 ! Hence the often rather sudden appearance of such organisms in huge numbers in small pieces of water. It is to be noticed that the protoplasm of the parent is entirely incorporated in the bodies of its offspring, the dead cell-membrane alone remaining behind ; but for the destruction of a large proportion, such organisms might be regarded as potentially immortal, in the sense that death from senile decay is unknown.

The normal green colour of the individuals of *Sphaerella* is often obscured by the accumulation of a bright red pigment (hæmatochrome) which appears particularly at certain times, when, with the withdrawal of the cilia and formation of a new membrane around the contracted protoplast, the individuals round off to form characteristic resting-stages (Fig. 100, B). If these occur in quantity they may lend a deep red colour to the water or mud.

For a long time multiplication may be purely asexual, but sooner or later—usually when growth is checked by a deficiency in nutritive salts—another method of reproduction sets in. This too is accompanied by division, but the resulting segments are more numerous, 16 or even 32 (sometimes as many as 100 in *Sphaerella*), being formed; these are liberated as *sexual cells* or *gametes* (Fig. 101, *a*), which only differ from ordinary individuals in being considerably smaller and naked (*i.e.* devoid of a cell-wall).[1] They move for a short time, but soon meet in pairs, whose cilia become entangled, and thereafter a gradual fusion (Fig. 101, *b, c*) of the two protoplasts and of their nuclei takes place. There results a single cell (termed a *zygote*) which moves for a brief period with the aid of its four cilia (Fig. 101, *d*) and then comes to rest. The cilia are with-

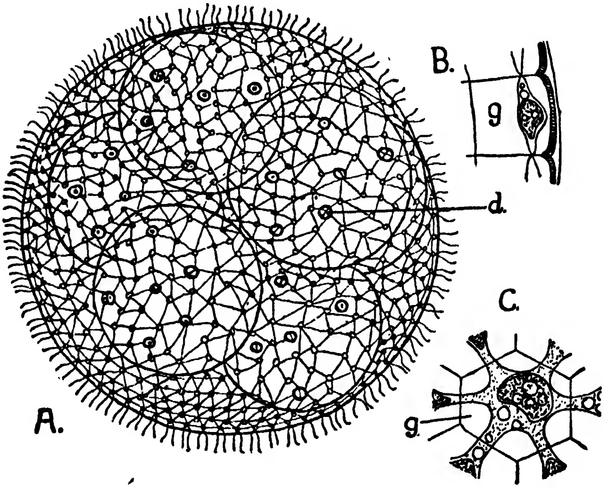

FIG. 102.—*Volvox*. A, Colony of *V. aureus* (after Klein) enclosing five daughter-colonies, the latter already exhibiting the large cells (*d.*) from which another generation will be developed. B, Section, and C, surface-view of single cells of *V. globator* (after Meyer). *g.*, mucilage-layer of cell-wall.

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[1] The sexual reproduction of *Sphaerella* is rarely observed and rather imperfectly known, and we have consequently described that of *Chlamydomonas*, which is probably similar in all essential respects.

drawn, the protoplast assumes a spherical shape and secretes a thick stratified membrane, and large quantities of a reddish-yellow oil appear in the cytoplasm. The resulting body (Fig 101, *e*) known as a *zygospore,* sinks to the bottom and enters upon a resting condition.

The process of reproduction just described is known as a sexual one since, as in all such processes, the fusing together of two distinct individuals is involved. Despite the fact that the gametes are outwardly all alike, there is evidently some internal (probably chemical) difference between them, for it has occasionally been observed that only gametes derived from distinct parent-individuals are attracted towards one another and fuse together.

Prolonged desiccation and extremes of temperature leave the thick-walled zygospores unharmed, even when the pool dries up. As the caked mud flakes and becomes powdery, both it and the zygospores are whirled away in windy weather as dust. If the zygospores are blown into water, their colour sooner or later changes to green, owing to the absorption of the yellowish oil, and the contents divide successively into a small number of parts which are liberated as new organisms by the bursting of the thick membrane. It is in this way that *Chlamydomonas*, *Sphaerella*, and similar forms reach, and develop in, almost any suitable piece of water.

The two genera just described are but representatives of a whole class of simple green plants, all of which swim about like animals during the greater part of their life,[1] and most of which are inhabitants of small pools and ditches. In some genera the unicellular individuals are combined in different ways to form definite groups or *colonies*, as in *Volvox* (the globe animalcule), sometimes found in large quantities in fresh-water. Here the colonies are composed of several thousand *Sphaerella*-like cells, and are of quite appreciable dimensions (usually about the size of a pin's-head) and readily visible to the naked eye (Fig. 102, A). New colonies are formed by the division of a few of the cells, and are at first liberated into the interior of the parent (Fig. 102, A) until set free by its rupture. *Volvox* thus affords a simple example of the setting apart of certain cells for special

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[1] In their mode of nutrition, however, they are altogether plant-like, and there is no justification for placing them in the Animal Kingdom.

purposes ; most are purely vegetative and perish with the death of the parent, whilst a few are destined to undergo division and survive as daughter-colonies.

A large proportion of the simple unicellular and colonial green plants are, however, non-motile throughout the vegetative phase of their life-history, and only exhibit movement, if at all, in connection with reproduction. As an example of a motionless unicellular plant, the very widely distributed *Pleurococcus*, which commonly forms the green powdery covering on tree-trunks, palings, etc.[1] may be studied. Under the microscope the green powder is seen to consist of small groups of 2, 4, or rarely more, cells, intermingled with which are more or less numerous rounded individuals (Fig. 103, A), all representing different stages of *Pleurococcus*. Each cell has a moderately thick wall, and contains a single nucleus and a lobed chloroplast (Fig. 103, B). The isolated cells constitute the adult form, and sooner or later divide, commonly by two successive walls at right-angles to one another, to form four-celled packets. Each daughter-cell is thus the quadrant of a sphere, but with subsequent growth it rounds off and separates from its neighbours, giving rise again to the adult form. This process of vegetative propagation is, when conditions are favourable, repeated at frequent intervals, and in this way *Pleurococcus* rapidly covers large areas.

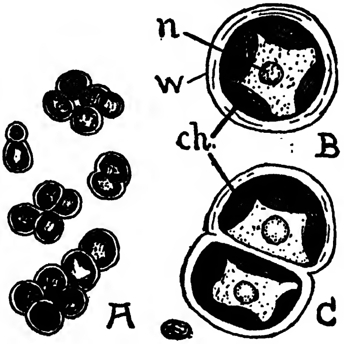

FIG. 103.—*Pleurococcus*. A, Group of cells, under the low power. B, Single cell, and C, pair of cells, under the high power. *ch.*, chloroplast ; *n.*, nucleus ; *w.*, cell-wall.

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[1] In these situations, however, *Pleurococcus* is invariably accompanied

The ordinary cells of *Pleurococcus* possess a remarkable power of withstanding drought, almost comparable to that of the zygospores of *Chlamydomonas* and other simple forms in which the vegetative individuals are extremely susceptible to adverse conditions. It is this property which enables *Pleurococcus* to exist, and even flourish, in the exposed dry habitats that it usually frequents. Although retaining its normal green appearance throughout the year, its activities are more or less completely arrested during prolonged periods of drought, when its only source of moisture is dew.

The organisms considered in the preceding pages of this chapter are simple representatives of a lowly group of the Vegetable Kingdom termed the *Algæ*, to which also belong the Pond-scums and the Seaweeds. A common example of the former is afforded by the genus *Spirogyra*, in which, as in all the Pond-scums, the plant consists of a filament or row of cylindrical cells. These are all nearly identical and of the type described on p. 62 (Fig. 33). The species of *Spirogyra* commonly occur as floating tangled masses in ponds and stagnant ditches, although some are found in flowing water, and they differ chiefly among one another as regards the number of spiral chloroplasts in the cells. Every cell is capable of performing all the life-processes (nutrition, growth, reproduction) and the only division of labour is seen in the occurrence of special attaching cells in early stages of development (cf. below). At times of active growth the threads not uncommonly break up into pieces or even into their constituent cells, each of which can divide to form a new filament, and such vegetative propagation is very prolific.

In sexual reproduction, which is of a peculiar type spoken of as conjugation and takes place most commonly in spring, two threads become ranged parallel to one another, and their opposing cells develop finger-like protrusions, the tips of which are in contact with one another (Fig. 104, B); after this the separating wall breaks down, so that an open tube (the conjugation canal, Fig. 104, *c.c.*) is established. The development of processes always commences a little sooner on the one filament than on the other, and a similar difference is observed with respect to the

by other unicellular green Algæ, some of which play a part in the formation of Lichens (p. 246).

contraction of the protoplasts which now ensues. The contents of the cells of the filament that first put out processes then commence to glide over, through the conjugation canals, into the opposite cells (Fig. 104, B, *b*), with whose passive protoplasts they fuse. In some species sexual union may take place between adjacent cells of the same filament (Fig. 104, A), the conjugation canals (*c.c.*) forming loop-like connections between their contiguous ends and one protoplast as before passing over into and fusing with that of the other cell. In view of this difference in behaviour between the two conjugating cells, they may, despite their identical form, be regarded as of opposite sexes, the active protoplast in this respect resembling a male and the passive one a female cell (cf. p. 230).

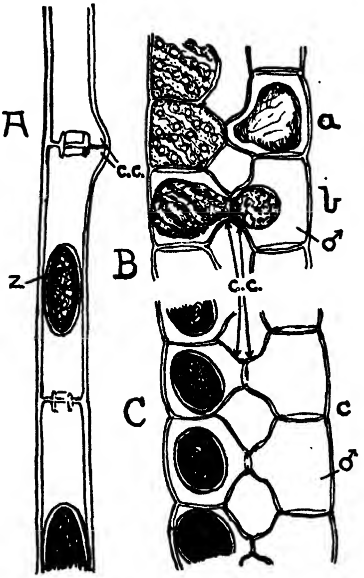

FIG. 104.—Sexual reproduction in *Spirogyra*. A, *Spirogyra weberi*, showing lateral conjugation (after Petit). B and C, *Spirogyra bellis*. B, successive stages (*a* and *b*) in conjugation; C, completed conjugation. *c.c.*, conjugation canal; *z.*, zygospore; ♂=male cells.

In all cases the zygospores (Fig. 104, *z.*) secrete a thick, several-layered wall, and, as the Alga dies away, they sink to the bottom. Here they may pass through a prolonged resting period, during which they may be distributed by the wind in the manner described for *Chlamydomonas.* On germination the membrane usually bursts at two places, the contents growing out in the one direction to produce the new filament, and in the other direction to form a colourless attaching cell. As the threads elongate, however, they soon break off from the attaching base, and thenceforward float freely.

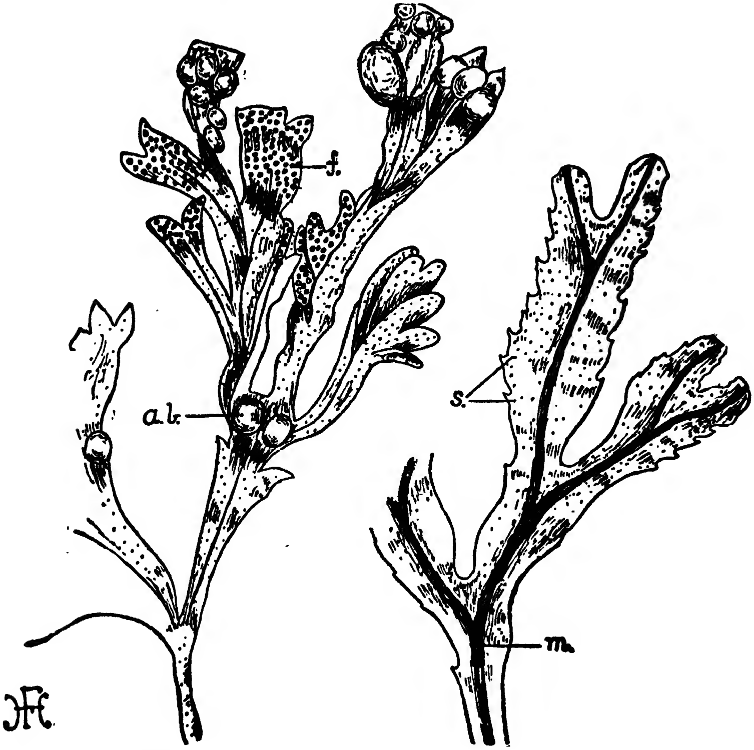

FIG. 105.—*Fucus.* On the left, part of a thallus of the Bladder Wrack (*F. vesiculosus*) ; on the right, of the Serrated Wrack (*F. serratus*). *a.b.*, air-bladder ; *f.*, fertile conceptacles ; *m.*, midrib of thallus ; *s.*, sterile conceptacles.

All the Pond-scums are filamentous like *Spirogyra*, although in some of them the filaments are branched. Many reproduce extensively by naked ciliate motile elements (zoospores), usually formed by subdivision of the protoplasts of the ordinary cells.

These, after a period of movement, settle down on some substratum and form new threads.

The bulk of the Seaweeds are massive multicellular plants of larger dimensions, and showing more marked division of labour than the Pond-scums. As an example, we may take the common Bladder Wrack (*Fucus vesiculosus*, Fig. 105), which is found on rocks between low and high tide-levels, so that it is uncovered for several hours at a time. An entire plant often attains a length of from one and a half to three feet, and exhibits three regions, viz., an attaching disc, a short stalk, and a repeatedly forked flattened frond (Fig. 105). Each portion of the last possesses an obvious midrib (*m.*), which is thicker and more pronounced in the older parts where it gradually passes over into the stalk. The latter is indeed nothing else than the persistent midrib of the first-formed part of the thallus. The paired air-bladders (Fig. 105, *a.b.*), which appear as occasional large swellings on either side of the midrib, and to which the specific name is due, increase the buoyancy of the plant when submerged, and may also, like the air-canals of aquatic Flowering Plants, serve for purposes of respiration. The brown colour of the thallus is due to the presence of a brown pigment masking the chlorophyll in the plastids and possibly serving to protect the latter from intense insolation.

Scattered irregularly over the whole surface of the frond are slightly protruding dots (Fig. 105, *s.*) marking the positions of small cavities (*conceptacles*) in the thallus. Usually some of the branches of the frond have swollen ends (Fig. 105) provided with much more conspicuous (fertile) conceptacles enclosing reproductive organs.

In transverse sections the globular cavities of the conceptacles (Fig. 106, A) are seen to be separated from the rest of the thallus by a wall (*w.*) composed of several layers of flattened cells, from whose inner surface arise numerous unbranched multicellular hairs which bend towards, and indeed often protrude from, the small aperture.

Interspersed between these hairs in the fertile conceptacles are special sexual organs in which the sexual reproductive cells are produced. The latter are of two kinds, male and female, which differ fundamentally from one another, as also do the structures in which they are formed. Those which give rise to male cells are known as *antheridia*, and those which produce female cells as *oogonia*. In the Bladder Wrack these two are found in distinct conceptacles, and on different plants, but there are other species of *Fucus* in which both occur in the same conceptacle.

The oogonia are prominent oval bodies, provided with a thick, transparent, several-layered membrane, and seated on a short stalk which arises directly from the wall of the conceptacle (Fig. 106, A). At maturity the contents are divided into eight uninucleate female cells or eggs (ova), containing abundant chloroplasts and separated by delicate septa. The antheridia are much smaller oval cells, which likewise possess relatively thick walls and occupy the ends of most of the short lower segments of richly branched hairs,[1] which occur scattered in between the unbranched ones mentioned above.

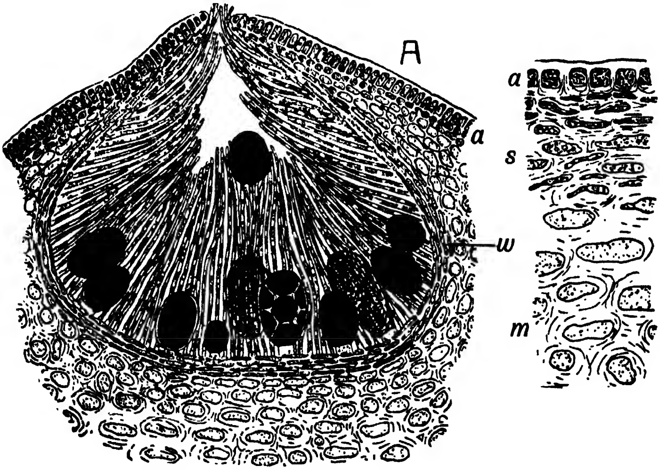

FIG. 106.—The Bladder Wrack (*Fucus vesiculosus*). A, Transverse section through a fertile conceptacle containing oogonia, in different stages of development. B, Small part of a transverse section through the thallus, more highly magnified. *a.*, assimilating layer ; *m.*, medulla ; *s.*, storage cells ; *w.*, wall of conceptacle.

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[1] These antheridial hairs are best examined by teasing out the contents of a male conceptacle in a drop of water.

In each are formed numerous minute biciliate male cells or spermatozoids containing a well-marked nucleus, but only traces of a chloroplast. The mature antheridia have a yellowish colour, which they impart to the entire conceptacle, and by this means the male plants can often be distinguished.

When the sexual cells are ripe, the outermost layer of the antheridium or oogonium, as the case may be, breaks open and sets free the contents which remain enclosed in the inner part of the wall. The gradual extrusion of these packets of ova, or spermatozoids, from the opening of the conceptacle often occurs between the tides, and is probably largely brought about by expansion of the mucilage, secreted by the hairs, combined with desiccation and contraction. The sea-water dissolves the membranes still enveloping the sexual cells, and the ova, which have now assumed a spherical form, become surrounded by the actively moving spermatozoids, which are no doubt attracted chemically[1] to the ova. Soon one of the spermatozoids penetrates into the egg and the cytoplasm and nucleus of the two fuse with one another. Neither sexual cell can develop independently of the other.

It is customary to speak of such sexual union as *fertilisation*, the egg being said to be fertilised by the spermatozoid. The effect of the fusion of a spermatozoid with an egg is probably of the nature of a chemical and physical stimulus, without which further development of the ovum is impossible. This view is supported by the fact that the eggs of Sea-urchins have been induced to develop into embryos by mere immersion in suitable solutions, whilst those of the Frog have been caused to undergo the first stages of development by mere pricking.

The fertilised egg or oospore secretes a thin membrane and immediately begins to develop into a new *Fucus*-thallus. The young plant is at first spherical, but at an early stage produces the basal holdfast and acquires a strap-shaped form, and this is soon followed by branching.

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[1] The influence exerted by chemical substances on the direction of movement of motile elements is spoken of as *chemotaxis*, and the positive chemotaxis evident in sexual union is only one of many examples of such chemical stimulation (cf. p. 235).

In the sexual reproduction of *Fucus*, as in that of all the more advanced forms of plants, there is thus manifestly a division of labour between the two gametes. Owing to its non-motile character the egg can possess a greater bulk and can therefore contain a more adequate supply of food-materials for the benefit of the next generation. Since the spermatozoids contribute nothing to this food-supply, they can be correspondingly smaller, and, therefore, without additional strain on the organism, produced in larger numbers, whereby the chance of fertilisation occurring is greatly increased. The probability of fusion between the two gametes is, moreover, doubled by one of them remaining stationary. The greater certainty of sexual union admits of a corresponding decrease in the production of eggs, which will afford as many offspring as would a larger number of motile female gametes.

In spite of the varied methods of reproduction with which we have become acquainted in this chapter the outcome is in all cases a cell capable of giving rise to a new plant, and it is this result rather than the means by which it is attained that must be regarded as the more important biologically.

CHAPTER XXIII

THE FUNGI

THE Algæ are not the only plants in which the body is a thallus of relatively simple construction, but the remaining representatives of the *Thallophyta*, the lowest class of the Vegetable Kingdom, are characterised by the absence of chlorophyll. They are, consequently, like the colourless saprophytes and parasites among higher plants, dependent upon organic material elaborated by other organisms. The plants in question are grouped as *Fungi* and show many peculiarities, both in vegetative structure and the nature of their reproductive processes.

A considerable number derive all their nourishment from other *living* plants or animals, such *parasites*, exemplified by the Smut of Wheat, the Gooseberry Mildew, the Potato Blight, the Salmon and Silkworm diseases, often doing serious harm to their host. Numerous Fungi, however, live upon decaying organic matter (*e.g.* many Moulds and Toadstools), and these *saprophytes* play an important part in nature in connection with processes of decay.

The plant-body is of a peculiar type, consisting generally of a loose weft, the *mycelium* (Fig. 109, *a*), composed of very delicate branched threads or *hyphæ*, which are usually colourless, and which may or may not be septate (Fig. 108, D, *a*). The narrow diameter of the hyphæ facilitates their penetration either into the interior of a host (parasites), or between the particles of decaying organic material (saprophytes). The hyphæ, moreover, secrete at their tips various enzymes (cf. p. 182), which bring about solution of the obstructing cell-walls and also convert the organic material into a readily assimilated form, a single species of Fungus producing a number of different enzymes, according to the substratum upon which it occurs. The extreme simplicity of the vegetative structure may well be compared with that of parasitic Flowering Plants (cf. p. 175).

Within the layer of cytoplasm lining the wall of each hypha there are, in the lower types (*Pythium, Mucor*), numerous minute nuclei, whilst in the septate hyphæ of the higher forms (*Penicillium, Agaricus*) there may be from one to several nuclei in each cell. Neither plastids nor starch-grains are ever present, but small oil-drops are often abundant. The central vacuole is prominently developed. Where abundant food-storage occurs, as, for instance, in the reproductive cells, it is customary to find the polysaccharide *glycogen*, which can be recognised by the deep brown colouration assumed with iodine.

Cystopus, a parasite which often attacks the Shepherd's-purse, is typical of some of the simpler plants (*Phycomycetes*) of this group, and the principal features of its life-history are, moreover, very easily studied. The parts affected by the Fungus, most commonly situated in the region of the inflorescence, are swollen and contorted (Fig. 107, A), and exhibit a white surface which looks as though it had been whitewashed. Such enlargement, or *hypertrophy*, is a frequent symptom of fungal attack, and is an outcome of the abnormal development of the diseased tissue, whose cells undergo increase in size with, or without, division. A longitudinal section through such a blister (best stained with eosin) shows the hyphæ within the intercellular spaces and middle lamellæ of the host. Here and there larger hyphæ bearing small club-shaped branchlets (the *haustoria*, *S.*, Fig. 107, B, *h.*) and belonging to another Fungus (*Peronospora parasitica*) will be observed in the actual cell-cavities, and by similar but finer hyphæ *Cystopus* absorbs food-material elaborated by the host.

Near the surface of the stem the hyphæ are more densely packed, and their almost parallel branches form a pile-like felt (Fig. 107, C) which ruptures the overlying epidermis and causes the white appearance above mentioned. The slightly swollen ends of these hyphæ exhibit various stages of constriction, resulting in the gradual formation of chains of spherical structures (*conidia*, *Sp.*), the oldest of which is farthest away from the point of origin. As the short fragile stalks connecting these reproductive bodies with one another get broken across, the latter are removed by the wind, and sometimes travel many yards before reaching the ground.

When rain or heavy dew causes a sufficient accumulation of moisture, the contents of these cells divide into several parts, which are liberated as minute colourless bodies (*zoospores*, Fig. 107, G), swimming by means of a pair of cilia. Many doubtless perish before reaching an appropriate host, but, should they

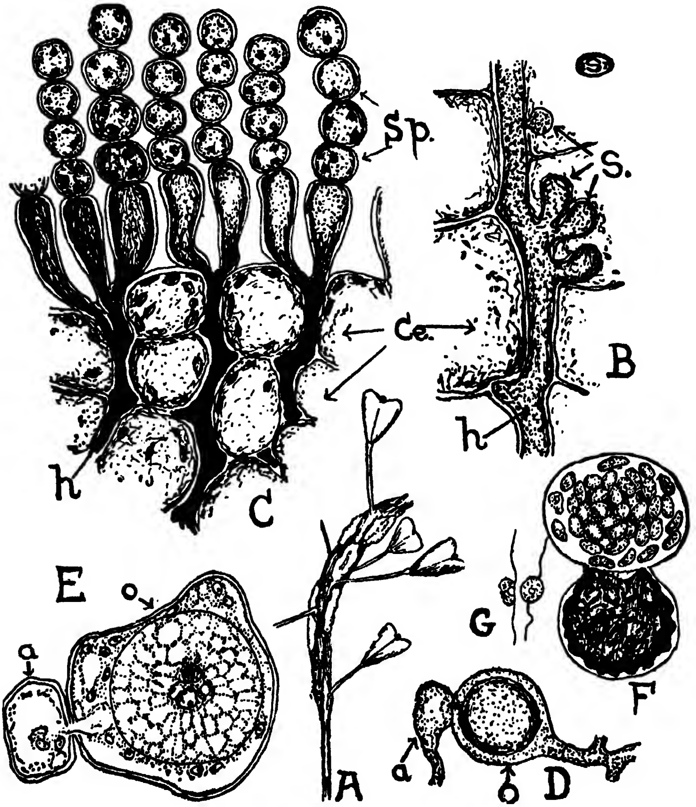

Fig. 107.—The White Rust of Cruciferæ (*Cystopus candidus*). A, Diseased inflorescence of Shepherd's-purse, showing the white patches where the conidia of the Fungus are being formed. B, Hypha (*h.*) of *Peronospora*, with haustoria (*S.*), in a longitudinal section between the cells (*Ce.*) of the host. C, Transverse section near surface of host, showing hyphæ (*h.*) and conidia (*Sp.*). D, Antheridium (*a.*) and oogonium (*o.*) (after De Bary). E, The same in section at the time of fertilisation (after Stevens). F, Germination of oospore (after De Bary). G, Zoospores (after De Bary). (Figs. A–C, original.)

encounter seedlings of a suitable plant, they come to rest on the surface, secrete a membrane, and elongate into a short hypha which penetrates into the interior by way of a stoma. The stimulus directing the movement of the zoospore towards the host-plant and the growth of the hypha into the interior is probably a chemical one (p. 230). For some weeks further development of the Fungus consists in the ramification and gradual spread through the tissues of the host, until a sufficiently large haustorial system has been created to supply the material necessary for the production of conidia.

Sexual reproductive organs are usually produced towards the end of the host's flowering period (*i.e.* when the supply of nutriment probably becomes deficient), and arise in the interior of the infected regions. They consist of spherical female organs, or *oogonia* (Fig. 107, D, *o.*), generally situated at the ends of the same hyphæ as bear the club-shaped male organs (*antheridia, a.*) at a slightly lower level, although in some cases the two structures are formed on neighbouring hyphæ. In both the greater part of the contents is used to form a single motionless gamete.

The antheridium becomes applied to the female organ and puts out a slender tube which, piercing the oogonial wall, penetrates through the peripheral cytoplasm up to the egg (female gamete, Fig. 107, D, E). The tip of the tube thereupon opens and the male gamete passes through it to fertilise the egg (cf. p. 230), the process involving nuclear and cytoplasmic fusion in the usual way. The product becomes invested by a thick dark-coloured wall (Fig. 107, F). After the decay of the host these *oospores*, which constitute the resting-stage in the life-history, may remain dormant in the soil for a considerable period. When conditions suitable for germination occur, the contents divide to form numerous zoospores which, after rupture of the thick wall, infect seedlings in the way already described.

The Potato Blight (*Phytophthora infestans*, Fig. 108, A) and the damping-off Fungus (*Pythium debaryanum*) have life-histories very similar to that of *Cystopus*. An attack by *Pythium* results in a rapid softening of the stems of the diseased seedlings (Fig. 108, B), which soon give way at this point and collapse. The diseased tissue is permeated by the branched unseptate hyphæ of the parasite, which, like *Cystopus*, forms its rounded asexual reproductive cells at the surface of the host. These are, however, borne singly on simple or forked hyphæ (Fig. 108, C) and usually give rise to zoospores without becoming detached, so that the disease rapidly spreads from one seedling to another; but under certain circumstances they may germinate direct to form a new plant. The sexual reproduction of *Pythium* is identical with that of *Cystopus*, the antheridia and oogonia again developing within the interior of the host.

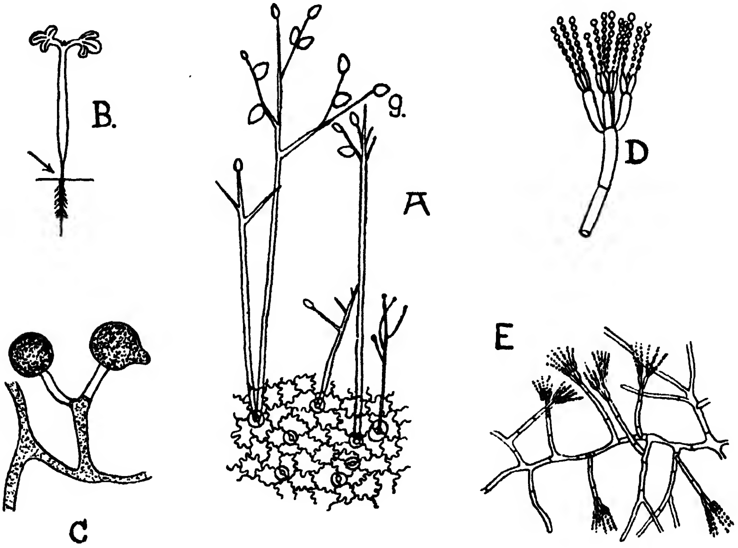

FIG. 108.—Asexual reproduction of various Fungi. *A*, Small part of epidermis of Potato-leaf, infected with Blight (*Phytophthora infestans*) showing branched hyphæ bearing conidia (*g*) emerging from the stomata. *B*, Seedling of Cress, which is "damping off," due to an attack of *Pythium debaryanum*; the point at which the hypocotyl is giving way is indicated by an arrow. *C*, Hypha with sporangia of the same. *E*, Small part of mycelium of *Penicillium* with conidia-bearing branches. *D*, One of the latter enlarged. (*A* after Strasburger, *B* after Miyaki, *C* after Hesse, *D* and *E* after Brefeld).

Owing to the ease with which the Fungi just considered produce zoospores, which of course require a film of moisture in which to swim, spells of damp, warm weather are particularly favourable to their spread and development. Indeed, the damping-off of seedlings through attacks of *Pythium* only occurs in conditions of excessive humidity due to overwatering or overcrowding.

A simple saprophyte among the lower Fungi is exemplified by the common *Mucor*, which thrives on all kinds of decaying substrata (especially horse-manure), upon which its mycelium forms a white weft (Fig. 109, *a.*). Numerous absorptive branches penetrate downwards into the source of nourishment, and sooner or later conspicuous, dark brown or black, spherical reproductive organs (*sporangia, sp.*) appear at the ends of relatively thick upright hyphæ. A kind of *Mucor* (*Rhizopus stolonifer*), that occurs very commonly on stale bread and horse dung spreads very rapidly by hyphæ resembling minute Strawberry runners, at the end of each of which a tuft of absorptive threads and sporangia is produced.

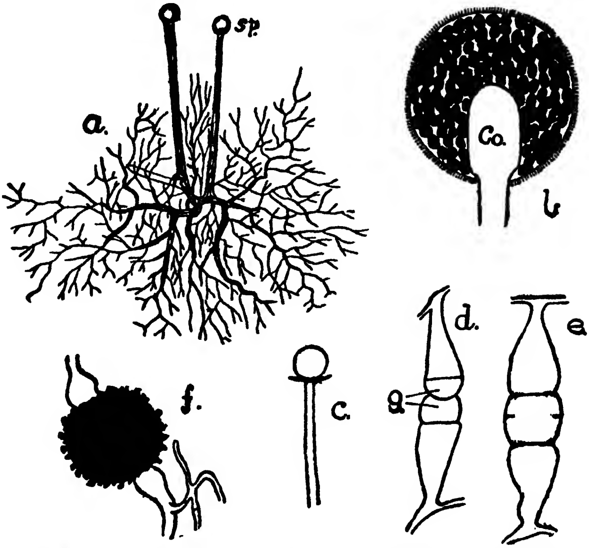

FIG. 109.—*Mucor*. *a*, mycelium, slightly magnified, showing two of the long-stalked sporangia (*sp.*); *b*, sporangium, much enlarged, in optical section, showing the numerous spores and the central column (*Co.*); *c*, dehisced sporangium in which only the column and a small part of the wall remains; *d* and *e*, conjugation of gametes (*g.*); *f*, mature zygospore. (*a*, *b*, and *f* after Brefeld; *c* after Sachs; *d* and *e* after De Bary.)

The wall of each sporangium (Fig. 109, *b*) is beset with numerous minute needles of oxalate of lime, whilst the swollen end of the hypha below projects into the cavity as a central column (*Co.*); between this and the wall are many small thick-walled spores embedded in a mucilaginous substance. The latter swells in the presence of moisture, and thus contributes to the bursting of the sporangium. It is also responsible for the adhesive nature of the spores, which are so widely disseminated by the wind that they are almost ubiquitous. They are extremely resistant, and are capable of remaining dormant for long periods. On germination they grow direct into a new plant.

Sexual reproduction in most species only takes place between two mycelia belonging to physiologically distinct strains, not distinguishable outwardly. The gametes are produced within swollen club-shaped branches whose end-portions become separated off by cross-walls (Fig. 109, *d*, *g*.). Two perfectly similar branches meet by their tips, one being derived from each of the two plants (Fig. 109, *d*), and the intervening membrane breaks down, whereupon fusion of the protoplasts and nuclei ensues (*e*). The product, deriving nutriment from the respective mycelia, subsequently undergoes slow enlargement to form a large spherical zygospore (Fig. 109, *f*). The latter on germination produces a short hypha terminating in a sporangium, some of the spores of which give rise to mycelia of the one and some to those of the other strain. The sexual process of *Mucor* is thus analogous to that of *Spirogyra*, where likewise an entire plant is often of one sex or the other (cf. p. 235).

A second great group of Fungi (*Ascomycetes*) is distinguished from the Phycomycetes by the method of spore-formation, and by the absence of a true sexual process in the vast majority of cases. A common parasite belonging to this group is the Ergot of Rye (*Claviceps purpurea*, Fig. 111, A), and there are numerous saprophytes, such as the ubiquitous Blue Mould (*Penicillium*) and the Cup-Fungi (*Peziza*).

The cup of *Peziza* represents the fructification of the Fungus, and arises from a mycelium, ramifying in the decaying substratum and similar to that of *Mucor*, but with frequent septa. A section of the cup (Fig. 110, B) shows it to consist of densely compacted hyphæ which, at the upper surface, form a very regular palisade-like layer (*h.*). A large number of the hyphæ in this layer develop as tubular sporangia (Fig. 110, A, *a-f*), each producing eight spores (ascospores), and sporangia with this constant number of reproductive cells are the most typical feature of the group of the Ascomycetes.

Ergot (*Claviceps*) infests the ovaries of Rye, Oats, and other Grasses, becoming very conspicuous at the time of harvest, as a result of the gradual replacement of the grains by a black banana-shaped mass (about half an inch long) of closely interwoven hyphæ (Fig. 111, A, *s.*). This constitutes a resting-stage of the Fungus, and is so hard that the term *sclerotium* is applied to it. The sclerotia drop off in the autumn and remain dormant in the soil until the following spring. Then they send up one or more stalked swellings (Fig. 111, D), in which are embedded numerous flask-shaped cavities (Fig. 111, E, *p.*) communicating with the exterior by small pores (Fig. 111, F). Each cavity is lined with sporangia similar to those of *Peziza*, each containing eight thread-like spores (Fig. 111, G), which are readily distributed by the wind. If caught by the stigma of a Grass-flower,

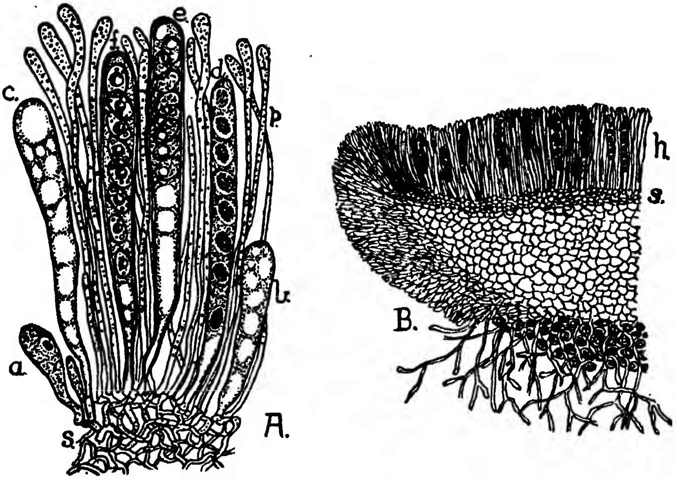

FIG. 110.—*Peziza vesiculosa.* B, Section of half a fructification (diagrammatic), and A, Small part of the superficial layer enlarged, showing sporangia in progressive stages of development (*a-f*). *h*, sporangial layer; *p.*, barren hyphæ of same. (After Goebel.)

the spores germinate, and the hypha grows down through the style into the ovary, thus bringing about a fresh infection.

By slow degrees the contents of the ovary are replaced by a dense hyphal mass with deep surface furrows (Fig. 111, B, upper part). From the ends of the superficial hyphæ, which are more or less parallel to one another, large numbers of minute gonidia are budded off (Fig. 111, C), and at the same time the surface secretes a sugary liquid. This attracts insects, to whose bodies the gonidia adhere, and so a rapid spread of the disease from flower to flower is brought about. Later in the summer, the outer hyphæ blacken, whereby the resting sclerotium is formed.

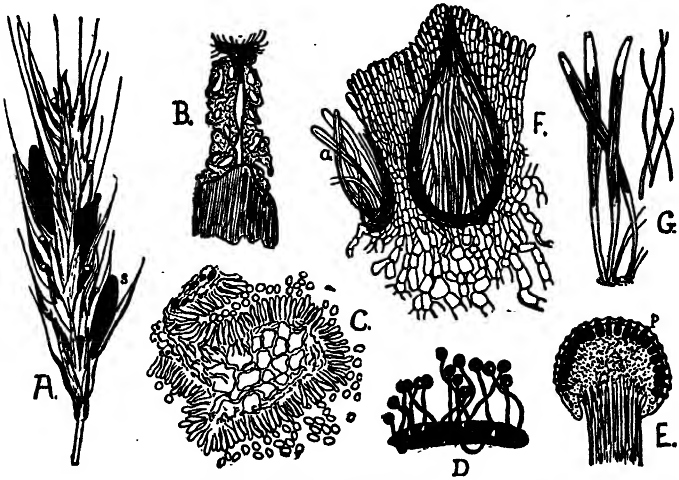

FIG. 111.—Ergot of Rye (*Claviceps purpurea*). A, Head of Rye, with a number of black sclerotia (*s*). B, Longitudinal section of ovary of Rye-flower, showing the dense hyphæ forming the sclerotium in the lower part, and the looser mass of hyphæ producing gonidia in the upper. C, A small part of the latter in section, highly magnified, showing the budding off of gonidia. D, Germinating sclerotium. E, Vertical section through one of the swellings arising from the latter, showing numerous flask-shaped reproductive organs (*p*), one of which is shown on a larger scale in F. *a*, sporangia. G, Three sporangia and (on the right) four of the thread-like ascospores. (A and D after Wettstein; the remainder after Tulasne.)

In some members of this group reproduction by gonidia is far more frequent than the formation of spores within a sporangium, as, for instance, in the common Mould *Penicillium* (Fig. 108, E). Here the gonidia are budded off in chains from the terminal branchlets of erect hyphæ (Fig. 108, D). Sporangia are occasionally produced in spherical fruits, which arise from special sexual organs, although it is doubtful whether any actual fusion of cell-contents occurs.

The *Rusts* constitute another group of Fungi which is of special importance as being the cause of many serious diseases of crops, and of these the Rust of Wheat (*Puccinia graminis*) is, unfortunately, all too common. Like many other members of the group, it possesses a very complicated life-history, whose phases, in this species, occur on two different hosts. In summer the parasite attacks the leaves and stems of various Grasses, and betrays its presence by the development of clusters of orange-coloured spores forming characteristic streaks upon them.

On the approach of winter, however, thick-walled resting-spores are formed which in spring germinate and give rise to reproductive cells, only capable of further development if they are blown on to the leaf of a Barberry. The spores produced within small cups upon the latter, on the other hand, can only germinate on the Wheat and certain other Grasses.

The existence of the Fungus on different host-plants, at different stages of its life-cycle, is paralleled among animal parasites (*e.g.* Malarial Parasite, Tapeworm), and suggests a means for the extermination of the disease, viz. by the eradication of one host. This is, however, only partially successful, since, under certain conditions, one phase in the life-cycle may be omitted.

The last great group of Fungi (*Basidiomycetes*) is likewise characterised by a special mode of spore-formation in which a definite number (usually 4) of spores is constricted off from the mother-cell. The common Mushroom (*Agaricus campestris*) affords a typical example. The mycelium, which inhabits soil rich in humus, and is present in considerable amount in so-called Mushroom spawn, is composed of binucleate cells. The hyphæ tend to be interwoven in bundles, so that the mycelium appears thicker and coarser than in Moulds. The overground edible portion is the reproductive body which first appears on the mycelium as a knob-like swelling (Fig. 112, *b*) composed of densely interwoven hyphæ, but later, as it gradually enlarges, broadens out at the top (Fig. 112, *c*, *a*). In the mature condition it consists of a stalk and an umbrella-shaped cap, with a large number of radiating plates or gills, which bear the reproductive cells on their surface. A little way below the cap the stalk is surrounded by a membranous ring of broken tissue (the *annulus*) which, before the expansion of the cap, extended continuously from the edge of the latter to the stalk, thus constituting a protection for the developing gills (Fig. 112, *a*).

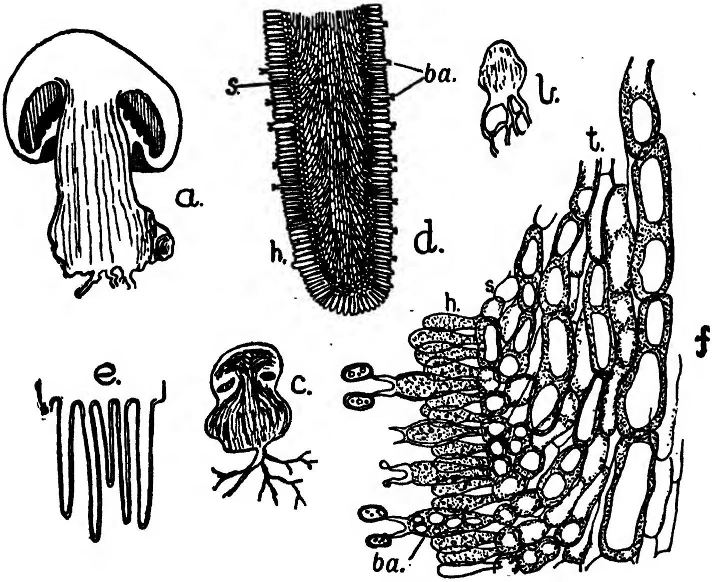

Fig. 112.—The common Mushroom (*Agaricus campestris*). *b*, *c*, and *a*, successive stages in the development of the fructification (in *a* the annulus is distinct, but yet unruptured); *e*, transverse section through small part of cap, showing gills; *d*, one of the latter enlarged; *f*, surface of a gill, in section, highly magnified. *ba.*, basidium; *h.*, hymenium; *t.*, large cells of middle of gill. (After Sachs.)

In a vertical section through the cap (Fig. 112, *e*) the middle of each gill (*d*, *f*) is seen to consist of longitudinally arranged hyphæ. These are composed of rather large cells (*t.*), and diverge at their ends to form the superficial palisade-like layer (*h.*). This comprises two kinds of club-shaped hyphal terminations; Some, the *basidia* (*ba.*), bear at their apex two, or four, short processes, from the end of each of which a basidiospore is formed, whilst the others are purely sterile, and probably play a part in the detachment of the spores.

The enormous production of spores in this and other similar Fungi can be gauged by placing the mature caps, with the gills downwards, on a sheet of white paper, when, after a short time, the outline of each gill will be marked by the spores which have been shed. It has been estimated that a moderate-sized specimen will produce some 1,800,000,000 spores!

Many of the Fungi play a very important rôle in the economy of nature. The *saprophytes*, in association with Bacteria, are largely responsible for the decomposition of vegetable remains, and without them the whole surface of the earth would become buried under the bodies of plants and animals. Through their agency the material locked up in the raw humus of the soil is transformed into simpler chemical compounds, and again rendered available for the use of higher plants. The processes of decay initiated by saprophytes are, however, often detrimental to the interests of man, as in the case of the "dry rot" of timber (*Merulius lacrymans*), and the diverse and almost ubiquitous Moulds which all too readily develop upon articles of food.

The *parasitic species* frequently do great damage to cultivated plants and to animals. In some cases the parasite sooner or later brings about the death of its host (*e.g.* Silver-leaf Disease of Plum), but more commonly (*e.g.* Rust) the diseased plant, though injured, continues to live as an unhealthy individual and to maintain the parasite which grows at its expense. A considerable number of parasites can also exist as saprophytes, so that they remain alive after the host has died (*e.g. Pythium*). Conversely, certain saprophytes (*e.g. Mucor*) can occasionally act as parasites, generally after access has been obtained at a point of injury. The so-called wound-parasites (*e.g. Nectria*, a species of which causes Coral-spot Disease of various trees) belong to this category, though their saprophytic phase is of short duration. The majority of Fungi, however, are either strictly saprophytic or strictly parasitic.

In many cases special conditions, such as excess of moisture (*e.g. Pythium*), the general state of health of the host, or accidental injuries to the latter, may be instrumental in bringing about the attacks of parasitic Fungi. Epidemics of such widespread diseases as the Potato Blight and the Gooseberry Mildew have, for instance, often been associated with particularly damp warm seasons. Fungi proper are rarely the cause of disease in man, but it may be mentioned that various skin diseases (*e.g.* Ringworm, *Favus*) are due to these organisms.

A particular species or strain of Fungus may be so specialised as to be able to attack only one particular kind of host, and of this the Rust-Fungi afford especially good examples. There is even often a difference with regard to *susceptibility* to a certain disease, between the various races of a cultivated plant; for instance, some varieties of Potato and Wheat are immune to Blight and Rust respectively, and would tend to be grown in regions in which these Fungi were known to be prevalent. Much has also been done by the production of immune hybrids (cf. p. 327) between immune and non-immune races. The ravages of a disease may decrease in intensity after it has been rampant for some years, the host presumably becoming adapted to the presence of the parasite; thus the Hollyhock Rust (*Puccinia malvacearum*), when first introduced into Europe about 1870, played great havoc with its host; but now, though Hollyhocks are still commonly attacked, they do not appear to suffer appreciably.

Fungi are, however, not only of importance in causing decay and disease, but also afford several greatly prized articles of diet (*e.g.* Mushrooms, Truffles, etc.), although their actual food-value is probably small. The great majority of the British Basidiomycetes are innocuous, but there are a certain number of species, some very widely distributed, which harbour deadly *poisons* (alkaloids, etc.), and attention may be drawn to the fact that such Fungi are by no means always highly coloured. Fungi are not often employed in medicine, except for the powdered sclerotium of the Ergot (*Claviceps*) which contains a nitrogen base having the property of causing muscular contraction.

The production of most alcoholic beverages is due to the activity of Yeasts (*Saccharomyces*), which are in all probability members of the Ascomycetes. The Yeast-plant (Fig. 113) consists of oval cells, which are either isolated (*a*) or adhere together in short chains (*c*), each the product of a peculiar method of division of a single individual. The thin-walled cells contain a large central vacuole (Fig. 113, *e*, *va.*), and, in contact with the latter at one point, a body resembling a nucleolus with surrounding chromatin (*n*), which become apparent on staining the living cells with a dilute aqueous solution of methylene blue ; vacuole, nucleolus, etc., together probably represent the nucleus. The Yeast-cells often contain large glycogen-vacuoles (*g.*), as well as small bodies (*v.*), stained deeply by methylene blue, and known as volutin-granules, which appear to constitute another kind of reserve.

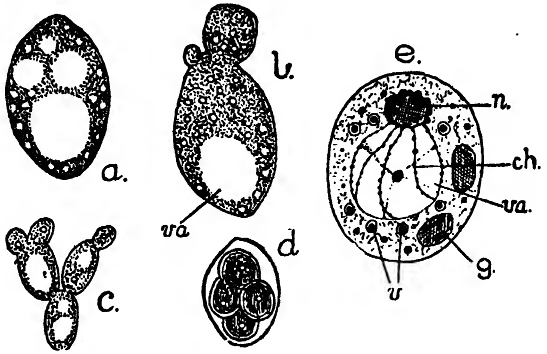

FIG. 113.—Yeast (*Saccharomyces*). *a–c*, various individuals, showing general form and multiplication by budding ; *d*, individual containing ascospores ; *e.*, cell-structure. *ch.*, chromatin threads ; *g.*, glycogen vacuole ; *n.*, nucleolus with surrounding chromatin ; *v.*, volutin granules ; *va.*, nuclear vacuole. (*a–d* after Wettstein ; *e* after Wager.)

When a cell has reached a certain size, it gives rise to a small outgrowth (Fig. 113, *b*) which slowly enlarges and assumes the form of the parent, from which it becomes separated by gradual constriction ; if this process of *budding* takes place rapidly, the cells do not immediately separate, and thus the chains (Fig. 113, *c*) are formed. A resting stage also occurs, as when Yeast is grown on the surface of a raw Potato ; under these circumstances the cell-contents undergo division into two or four parts, each surrounded by a thick wall (Fig. 113, *d*). This formation of spores may be preceded by conjugation of Yeast-cells.

There are a number of different species of Yeast which ferment various sugars and split them up into alcohols (mainly ethyl alcohol) and carbon dioxide. The chemical change is brought about by an enzyme *zymase* (cf. pp. 183, 184) which can, with some difficulty, be extracted from the cells; in addition the latter contain invertase and other ferments. The mode of action of zymase is complicated and not yet fully understood, but it is known that *fermentation* depends on the contemporary presence of phosphates (cf. p. 186). The alcohol present in beer, wine, etc., is formed by the action of Yeasts, while the carbon dioxide simultaneously evolved is compressed into cylinders and sold as a by-product. In the manufacture of beer, malt (*i.e.* germinated Barley) is treated with hot water, and supplies part of the sugar, various other sugars being used according to local practice. Hops are added to the liquid to provide the peculiar flavour, and the whole of this wort is then fermented in vats.[1] The success of brewing depends upon the employment of pure races of Yeast and the realisation of the right temperatures at the different stages of the process; a small supply of Oxygen has also been shown to be favourable to active fermentation.

The energy liberated in the fermentation of sugars enables Yeast to thrive and grow when, apart from the sugars, only inorganic food-materials are supplied. Here therefore chemical energy is utilised in synthesis.

We have already noted that a parasitic Fungus may sometimes do very little harm to the host, and such cases are but a step removed from those in which the balance, between the Fungus and the organism with which it is associated, is so perfect that both are mutually benefited. Such a condition is found in the *Lichens*, whose body is composed of algal cells embedded in a weft of fungal hyphæ; the latter are usually especially densely packed near the surfaces of the thalli, whose outline is generally entirely determined by the Fungus. Lichens, with but few exceptions, are subaerial, being commonly found on peaty soils, rocks, tree-trunks, old walls, etc. The Algæ found within

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[1] If all the starch in the malt is allowed to undergo conversion into sugar, and the fermented product is distilled, whisky results; brandy is similarly obtained by distilling the alcohol from fermented grape-juice.

Lichens are forms which can also grow independently in the terrestrial habitats in which the latter occur. The Fungi concerned are, on the other hand, unable to lead a separate existence in nature, and are only capable of growth when associated with their appropriate Alga.

As a result of the association of the two organisms, the Alga obtains protection and a supply of moisture, whilst the Fungus no doubt profits by absorbing part of the photosynthetic products of the Alga, with whose cells some of its hyphæ come into intimate contact.

FIG. 114.—Iceland Moss (*Cetraria islandica*), part of a large specimen about natural size.

The co-operation between Alga and Fungus in Lichens is paralleled by the so-called "green cells" found in several aquatic animals (*e.g.* Freshwater Sponges, *Hydra viridis*); these are due to unicellular Algæ, and in all such cases the partnership between plant and animal appears to be of mutual benefit.

The bright colours of many Lichens are due to the presence of pigments which are remarkable for their "fast" character, and have been employed in dyeing. The well-known chemical indicator litmus is obtained from species of *Roccella*. Iceland Moss (*Cetraria islandica*, Fig. 114), which forms a slimy fluid when boiled with water, is used as an invalid food.

CHAPTER XXIV

THE BACTERIA

THE *Bacteria* constitute an extremely important group of Thallophyta whose relationships are very obscure. It is perhaps almost unnecessary to emphasise the fact that these minute organisms are not members of the Animal Kingdom, an error which is nevertheless not infrequent in the popular conception of germs. Their plant character is evidenced, not by the possession of any green colouring matter, since all Bacteria are parasites or saprophytes, but by the mode of nutrition, food being taken in as a solution. Moreover, their reproduction takes place entirely by vegetative means, mere cell-division being by far the commonest method of propagation, a feature more characteristic of the Vegetable than of the Animal Kingdom. By contrast with the very simple internal structure referred to below, the Bacteria exhibit a high degree of physiological specialisation in relation to the dead or living organic material upon which they live (cf. p. 251).

The majority of species are colourless unicellular forms of extremely small size. The larger specimens are not more than 1/100th mm. in length, and about one-tenth as wide, whilst the globular forms average 1/1000th mm. in diameter. Some are so small as to be almost, if not quite, invisible under the highest powers of the microscope. They occur in almost every possible situation, and live under the most varied conditions. They are not killed by cold, and some can survive for many months at the temperature of liquid air. Whilst most die if heated to about 50° C., a few (*thermophilic Bacteria*) live in fermenting hay and manure heaps which, owing to their activity, may attain a temperature of 70° C.[1] Many Bacteria also inhabit the waters of hot springs.

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[1] Hence the employment of manure for hot-beds, etc.

Bacteria are rod-shaped (*Bacillus*, Fig. 115, *d*, *f*, *Bacterium*), spherical (*Micrococcus*), or curved (*Spirillum*, Fig. 115, *k*). The rod-shaped individuals may be joined end to end to form long filaments (Fig. 115, *d*), whilst the *Coccus*-forms may occur in chains (*Streptococcus*, Fig. 115, *b*), in cubical packets (*Sarcina*), or in irregular masses (*Staphylococcus*, Fig. 115, *a*). The individuals may be capable of movement owing to the possession of cilia, which are only visible after careful staining, or they may be devoid of these, and exhibit Brownian movement (cf. p. 71) in correspondence with their minute dimensions. In the elongated forms the cilia are either situated in tufts at the two ends (*Spirillum*, Fig. 115, *k*), or else arise all over the body (*Bacillus*, Fig. 115, *e*, *f*), but there are some genera possessing only one or two cilia restricted to one end of the cell (*Pseudomonas*, Fig. 115, *l*).

Very little is known regarding the internal structure of the cells, and it is a matter of doubt whether or not they possess a true nucleus; plastids are of course absent. The cell-wall appears to consist of a protein, and may probably be regarded merely as a differentiated outer layer of the cytoplasm. The latter contains various substances, of which the commonest are glycogen (cf. p. 233), granules of volutin (p. 245), and fat-globules which appear as brighter specks in the cytoplasm.

Multiplication of the cells by *division*, under normal circumstances, ensues with great rapidity, often taking place once every hour, or even more frequently. In some of the elongated forms the daughter-individuals are separated off by a mere constriction of the cell (*e.g. Bacterium* spp.), whilst in other cases the latter is subdivided by a transverse septum which subsequently splits down the middle. In certain Bacteria inhabiting water or other fluids, the daughter-individuals develop thick mucilaginous walls, and in consequence adhere together in vast numbers to form an often iridescent pellicle on the surface, or thick pale-coloured floating masses (*zooglœa-stages*).

Bacteria survive unfavourable conditions by the formation of resting *spores*, produced within the cells by a localised concentration of the greater part of the protoplasm, which then stains differently to the peripheral portion. This central region eventually becomes surrounded by a thick wall, and at maturity the remainder of the cell is often empty (Fig. 116, *b*, *c*). The spores are frequently located in special parts of the cell, giving the spore-forming individuals a characteristic appearance, as in *Bacillus tetani*, where they occupy a dilation of one end (Fig. 116, *a*). In certain forms (*e.g. Bacillus amylobacter*) more than one spore may be developed by each individual. Bacterial spores are often very resistant to extremes of temperature, and can indeed in some cases (*e.g. Bacillus subtilis*) withstand prolonged boiling.

Most sorts of Bacteria live a free life in water, earth, etc. Many exert a very beneficial action in promoting decay and maintaining the circulation of nitrogen and carbon dioxide in nature, whilst a small number are extremely harmful, living as parasites on higher animals and plants, and causing such diseases as typhoid, cholera, plague, etc. Whilst some, such as *Bacillus subtilis*, which is found in infusions of hay, etc., require a free supply of Oxygen (aerobic species), others, such as the organism responsible for lock-jaw (*Bacillus tetani*), will grow only in the almost complete absence of Oxygen (anaerobic species). Hence the value of oxidising agents (*e.g.* many antiseptics) for the cleansing of wounds.

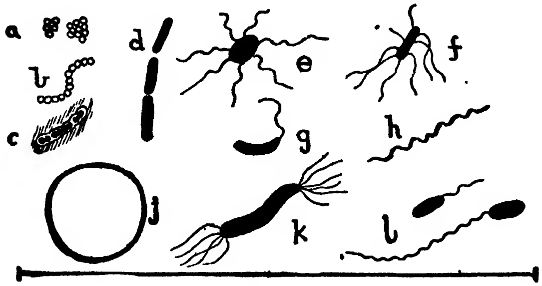

FIG. 115.—Various Bacteria (magnified about 1,000 times). *a*, *Staphylococcus aureus* ; *b*, *Streptococcus pyogenes* ; *c*, *Pneumococcus* ; *d*, *Bacillus anthracis* ; *e*, *B. typhosus* ; *f*, *B. tetani* ; *g*, *Microspora comma* ; *h*, *Spirillum* of relapsing fever (possibly Protozoal) ; *k*, *Spirillum rubrum* ; *l*, *Pseudomonas* spp. *j* represents a blood corpuscle on the same scale, and the line below, the width of a fine human hair, or about half the thickness of a sheet of newspaper. (*a–h* from Muir and Ritchie; *k–l* after Engler and Prantl.)

It will be realised that the identification of the *pathogenic forms* (*i.e.* those causing disease), in particular, is of great importance. Owing, however, to the small dimensions of the individuals, it is as a rule impossible to identify the species by microscopic examination alone. Resource is therefore had to the various reactions of Bacteria under conditions of culture.

Bacteria can be grown in the laboratory on various artificial media, such as extract of meat, decoctions of fruit, etc. Under such conditions, and at temperatures suitable for each species, growth is very rapid, and a single organism soon multiplies to such an extent that the mass of its offspring is visible to the naked eye. In making cultures all the vessels and instruments employed are scrupulously cleaned and freed from live Bacteria (*sterilised*), either by heating at high temperatures or by washing with special disinfectants, since even small quantities of dust are replete with bacterial spores.

The different kinds of Bacteria present in any material to be examined can be separated from one another and isolated by using the various culture media mentioned above, with the addition either of gelatine or agar-agar. A little of the material containing the organisms is well mixed with a considerable quantity of such a medium, liquefied by warming, so that the individual bacilli are widely separated from one another. On allowing the mixture to cool the Bacteria are immobilised; they soon grow, and each of the widely separated individuals gives rise to a small group (colony), visible to the naked eye, which can be transferred to another lot of culture medium. In this way cultures can be obtained which have arisen from single organisms and consist of one species only (*pure cultures*); in them the form of the Bacteria, their mode of growth, the formation of pigment (usually outside the cells) and other chemical substances, can be studied and the species identified.

Some Bacteria are entirely parasitic (*e.g.* the *Micrococcus* which causes spotted fever) and cannot live apart from their host, whilst some are semi-parasitic (*e.g. Bacillus tetani*) and can live either in earth, etc., or in the body of a Mammal. Each parasitic species can generally use only one or two species of Mammal asativts (cf. p. 244); thus, children do not have distemper, and dogs and cats do not have measles and chicken-pox.

Similarly *Bacillus carotovorus* causes " soft rot " of Carrot, but does not attack Parsnips.

The evil effects of parasitic Bacteria are due to poisons (*toxins*) which they produce ; these are proteins in nature, and those which have been isolated are the most poisonous chemical substances known. The infected animal resists the invading organism, partly by the amœboid cells of the blood (leucocytes) which devour them, and partly by producing chemical substances which neutralise the toxins. The power of the body to make a successful resistance is much improved by practice. Hence one attack of an infectious disease often enables a person to destroy that particular bacillus at once if it gets into the body a second time, and so another attack of the disease is avoided.

A large number of Bacteria obtain energy[1] by bringing about processes of *fermentation*. Thus the Vinegar Bacteria (*Bacterium aceticum*, etc.) convert alcohol into acetic acid,[2] whilst the lactic acid Bacteria cause the souring of milk, changing the milk sugar (lactose) into lactic acid. Another product of bacterial activity is butyric acid, which is the chief cause of the rancid character of bad butter. The putrefaction of meat is likewise due to the agency of Bacteria, which in this case decompose protein substances. Each type of cheese is the product of a definite bacterial and Fungus flora. In many cases fermentation is due to a group of organisms ; for instance, the so-called ginger-beer plant, used in the manufacture of the beverage of that name, consists of a Yeast (p. 244) associated with certain Bacteria.

It is largely to Bacteria that we owe the decomposition of the cellulose in dead leaves, etc., whereby undue accumulation is prevented, and the carbon is again brought into circulation as carbon dioxide. The processes of decay involved in the " retting " of fibres (*e.g.* Flax, Hemp, Jute), the " curing " of tobacco, and the conversion of sewage are likewise brought about by members of this group.

The nitrates of the soil, upon which plants are dependent

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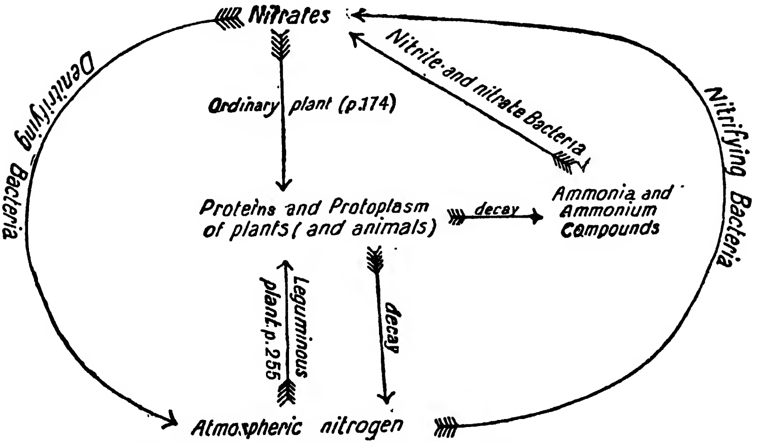
[1] In some cases part of this energy is dissipated as heat (cf. p. 248) or light (*e.g.* the phosphorescence of bad meat).

[2] In the commercial production of vinegar eit[illegible] or spirit is used as the raw material, and to these vinegar [illegible] order to introduce the necessary Bacteria.

for their supply of Nitrogen (cf. p. 169), are, owing to their ready solubility, continually being washed away, but the supply is always being replenished by the action of Bacteria. The decay of plant and animal bodies, which is likewise due to bacterial agency, leads to the production of a large number of waste products, of which one of the most important is ammonia. The latter combines with the calcium carbonate in the soil to form ammonium carbonate, and this is oxidised to a nitrite by the so-called *Nitrite-Bacteria* which belong to the genus *Nitrosomonas.* The nitrites in their turn are converted into nitrates by the *Nitrate-Bacteria* (*Nitrobacter*), and in this way the ammonia, liberated by the decay of dead organisms, again becomes available to living plants.



Scheme to explain the circulation of Nitrogen in nature.

By means of these oxidative processes the Bacteria in question gain the energy necessary for their vital activities. It has been found possible to cultivate them only in the absence of organic matter, but in nature the presence of the latter in the soil seems even to be beneficial. Nevertheless these organisms appear to be capable of building up organic substance from simple compounds, utilising for this purpose the energy obtained in the oxidative processes which they carry on. These nitrifying Bacteria cannot flourish in acid soils, or in such as contain an appreciable amount of free ammonia. This probably explains their paucity in many soils which are rich in humus (*e.g.* moorlands) or poor in lime. Where the decay of organic matter takes place on a large scale, as in the guano-fields of Chile, so large a quantity of nitrates may be formed that they accumulate as an efflorescence on the surface of the soil. This is the mode of origin of Chile saltpetre (potassium nitrate).

The beneficial action of these organisms is to some extent countered by the breaking down of nitrates with the evolution of Nitrogen by such Bacteria as *Bacterium denitrificans* (*denitrification*). There are, however, others (the *nitrogen-fixing* or *nitrifying Bacteria*), which actually have the power of fixing the free Nitrogen of the air, with the formation of organic Nitrogen compounds, although the chemical processes involved are obscure. The most important of the organisms concerned is *Azotobacter* (Fig. 116, *d*), an aerobic form which obtains its energy by the breakdown of carbohydrates, a process setting free a considerable amount of carbon dioxide. The amount of Nitrogen fixed is proportional to the amount of organic material decomposed. Another of the nitrogen-fixing Bacteria, *Clostridium pasteurianum* (Fig. 116, *e*), is anaerobic, the principal product of its activity, apart from nitrogenous compounds, being butyric acid. It is the organisms mentioned that are largely responsible for the gradual increase in the Nitrogen-content of unmanured grassland.

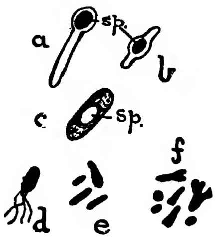


FIG. 116.—*a–c*, spore-formation in Bacteria. *a*, *Bacillus tetani*; *b*, *Bacillus* of malignant œdema; *c*, *Bacillus œdamitis*. *sp.*, spores. *d–f*, nitrogen-fixing Bacteria. *d*, *Azotobacter*; *e*, *Clostridium pasteurianum*; *f*, *Bacillus radicicola*. (After Engler and Prantl, and Ellis.)

There is thus a continual circulation of Nitrogen in nature (cf. the scheme on p. 253), and the different organisms concerned evidently work sufficiently well in unison to maintain the balance.

Even in the time of the Romans the inclusion of Leguminous plants in a rotation of crops was recognised as beneficial. Experience has shown that cultivation of Clovers, Sainfoin, Lucerne, etc., materially increases the Nitrogen-content of the soil, especially if the crop is subsequently ploughed into the field (so-called green-manuring). This phenomenon remained unexplained until it was discovered that the swellings upon the roots of Leguminous plants (Fig. 117) are inhabited by Bacteria (*Bacillus radicicola*, Fig. 116, *f*), capable of fixing free Nitrogen and present in every healthy soil. Infection of the root takes place through the root-hairs, probably when the organism is in the motile phase; having penetrated the root-hairs, the Bacteria pass into the adjoining cells, which are thereby caused to divide, so that a gall-like structure arises. Within the cells of this nodule rapid multiplication of the Bacteria ensues, probably at the expense of carbohydrates furnished by the Leguminous plant. At the same time, however, the latter profits by the nitrogenous material formed by the Bacteria, the removal of which is indeed necessary for their continued activity. In the mature condition large numbers of the Bacteria, within the cells of the nodules, assume an irregular form, and become digested by the action of the host. A limited number persist unaltered, and return to the soil as the roots decay away.

The relation between the nodules and these nitrogen-fixing Bacteria is shown by the fact that Leguminous plants, grown from seed in soil which has been thoroughly sterilised by heating, fail to develop any nodules, and are just as dependent on a supply of soil-nitrates as other green plants. It appears that different strains of these Bacteria infect different Leguminous plants, and that normally those of a particular strain only attack other individuals of the same species.

The presence of Bacteria in the soil can be demonstrated in the following way: Three clean Petri-dishes, sterilised by placing them in boiling water, are filled with a solution of gelatine (10 parts of gelatine to 100 of water). A little garden earth is then taken and divided into two parts, one of which is thoroughly baked; thereupon each lot of soil is shaken up with boiled water which has cooled and a few drops from each liquid is added to distinct dishes of the gelatine just before setting. The third dish is left untreated as a control, all three being covered. After some days the gelatine to which water from the unbaked soil was added will show a number of white bacterial colonies, whilst few or none are to be seen in the other two dishes.

Fig. 117.—Root-system of the Meadow Vetchling (*Lathyrus aphaca*), showing the root-tubercles (*t*) (natural size). The level of the soil is indicated by a dotted line.

In conclusion, brief reference may be made to the so-called *Thread-Bacteria*, whose exact relation to the other forms is, however, dubious. A common form, *Beggiatoa*, is frequent in waters rich in sulphuretted hydrogen; the organism in question obtains the energy necessary for the building up of organic substances by the oxidation of the sulphuretted hydrogen to sulphur. The Iron-Bacteria (*Leptothrix*, *Crenothrix*, etc.), whose branched threads are abundant in ferrugineous waters, and which are often the cause of the brown deposit of ferric hydroxide, are further examples of these forms.

CHAPTER XXV

MOSSES AND LIVERWORTS

IN Liverworts (Hepaticæ) and Mosses (Musci), which are classed as *Bryophyta*, the sexual organs are of a more elaborate kind than in Thallophyta (Algæ and Fungi). The plant-body, moreover, usually exhibits greater complexity of structure, which may be related to the fact that the Bryophyta are on the whole terrestrial plants in contrast, for instance, to the essentially aquatic Algæ.

The majority of Liverworts, however, frequent damp places, many of them growing in situations that are covered with moisture in the wetter seasons (*e.g.* along the sides of water-courses). Many Mosses, on the other hand, can flourish in habitats that are comparatively dry for a great part of the year, an extreme example being furnished by the Wall Moss (*Tortula muralis*, Fig. 118, D), common on old walls, buildings, etc. In relation to this difference of habitat, Mosses generally display a structure which is more elaborate, and better suited to resist drought, than that of Liverworts.

Mosses (Fig. 118) possess a definite stem, bearing three or more rows of alternate sessile leaves, and in this respect they contrast with many Liverworts where the body is a flat, ribbon-like thallus. The lower part of the Moss-stem, which is buried in the soil, forms a kind of rhizome bearing numerous hair-like *rhizoids*, and sometimes small scales as well. The rhizoids, which may also develop from the part of the stem just above the soil, are organs for the absorption of moisture and also function for attachment. They are outgrowths of the superficial cells, like those of Liverworts (Fig. 120, A, *r*.), but differ in being multicellular and branched; they usually have brown membranes, and are divided by oblique septa, just behind which the branches originate.

The leaves of Mosses are attached to the stem by a broad cushion-like base, and usually, except in the region of the midrib, which forms a strand of narrow, elongated elements, consist of a single layer of cells. The presence of a midrib forms a point of contrast with the leafy Liverworts. The branches of the stem arise from below the leaves, and are produced in such large numbers from the base, in some of the erect forms, that the plants exhibit a densely tufted habit (*e.g. Tortula,* Fig. 118, D). The stem invariably contains a distinct central conducting strand, composed of small, thin-walled, much elongated cells, but true vascular tissue is not differentiated.

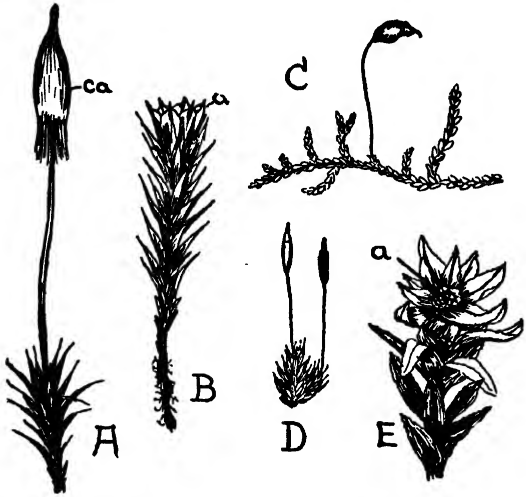


Fig. 118.—Various Mosses. A, Plant of *Polytrichum,* bearing a sporogonium whose capsule is covered by the calyptra (*ca*). B, Male plant of the same, showing the antheridial head (*a*). C, *Hypnum,* with sporogonium. D, *Tortula muralis.* E, Male plant of *Mnium,* with antheridial head (*a*).

Both Liverworts and Mosses propagate abundantly by vegetative means, most frequently by fragmentation of the thallus. At certain times, however, they produce *sexual organs,* which develop especially in the spring, the male being known as antheridia and the female as archegonia.

The antheridia of Mosses (Fig. 119, *a*) occur in groups, interspersed with multicellular sterile hairs (*p*), at the top of the stem or its branches. Each antheridial group is surrounded by a number of spreading protective leaves (*involucre*), which are not infrequently arranged to form a kind of cup, and usually differ in shape and size, and sometimes also in colour, from the ordinary leaves. The male plants of Mosses are thus easily recognised (Fig. 118, B and E). Each antheridium possesses a single-layered wall and at maturity encloses a dense mass of small, colourless, closely packed cells, the spermatozoid mother-cells (Fig. 119, *a*), each forming within itself a single male cell or spermatozoid. Rupture of the antheridium takes place in wet weather through vigorous absorption of water by the wall, the contained mass of mother-cells often being ejected to some slight distance. The membranes of the mother-cells then become dissolved, thus setting free the spermatozoids, which possess a spirally coiled body composed mainly of a large nucleus and bearing two long cilia at the slightly tapering front end.

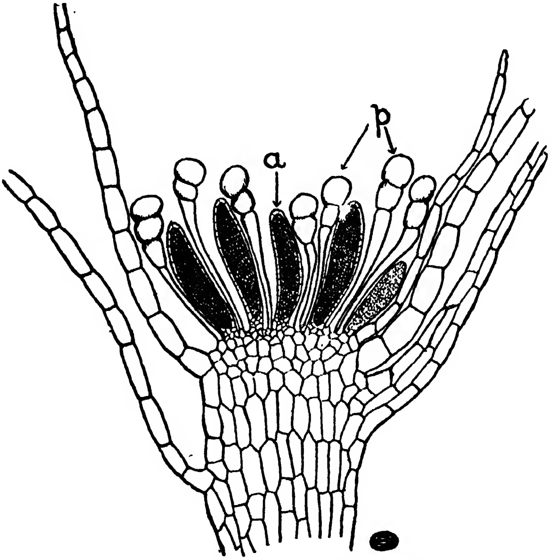


Fig. 119.—Vertical section through the antheridial head of the Moss *Funaria*, showing the antheridia (*a*) and interspersed sterile hairs (*p*).

The archegonia of Mosses likewise occur in groups, interspersed with sterile hairs, at the top of the stem or its branches, but such groups are not as easily recognised as the antheridial ones. The archegonia are flask-shaped structures (cf. Fig. 120, B, of a Liverwort), composed of a lower swollen part, or *venter* (*v*), and a long neck (*n*), which is often twisted. The neck is a tube consisting of a single layer of elongated cells surrounding a narrow canal. The latter is occupied by a row of naked *neck-canal cells* which ultimately become mucilaginous, and, in swelling, push apart four lid-cells which, till then, close the upper end of the neck-canal. Within the wall of the venter (Fig. 120, B) is the large naked female cell or egg (*e*), with a small *ventral canal cell* (*v*) at the base of the neck.

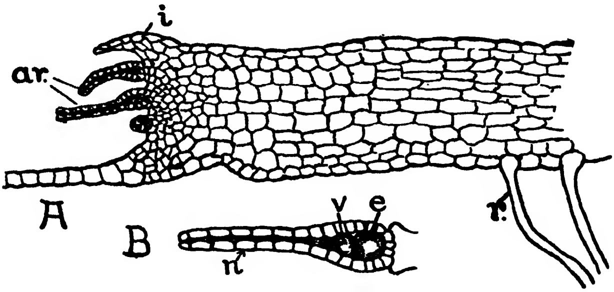


FIG. 120.—A, Longitudinal section through the apex of the thallus of the Liverwort *Pellia*, showing a group of archegonia (*ar*), and the involucre (*i*). *r*., rhizoid. B, single archegonium of *Marchantia*, on a larger scale. *e*, egg ; *n*, neck ; *v*, ventral canal cell.

The branches bearing the archegonial groups are at first usually short and adjacent to the soil, so that they are readily covered with moisture during rain. After escaping from the antheridia, the spermatozoids, swimming in these surface films of moisture, are chemically attracted to the open necks of the archegonia by cane-sugar contained in the mucilage formed by the breaking down of the canal cells. The spermatozoid passes down the neck-canal and enters the egg, after which nuclear fusion occurs.

The fertilised egg secretes a cell-wall and, without any resting-stage, commences to divide and grow into a new Moss-plant. This, however, differs fundamentally from the parent, especially in being parasitic upon the latter, and at maturity constitutes an organism (the *sporogonium*, Fig. 118, A, C, D) that is almost solely concerned in the production and dispersal of spores. This simplicity of structure can possibly be related to the parasitic habit, thus affording an interesting analogy to parasitic Flowering Plants. As the embryo develops from the fertilised egg, the venter of the archegonium stretches and grows into a protective covering, the *calyptra*, which can often be recognised around the young sporogonium.

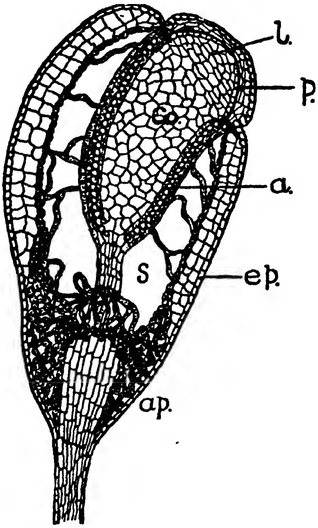


Fig. 121.—Longitudinal section through young capsule, apophysis (*ap.*), and the top of the stalk of the Moss-sporogonium (*Funaria hygrometrica*, after Sachs). *a.*, archesporium; *Co.*, columella; *ep.*, epidermis; *l.*, lid; *p.*, peristome-layer; *S.*, air-space.

The embryo elongates considerably at an early stage, and soon acquires the shape of a rod tapering at either end. The lower extremity penetrates into the tissue of the Moss-stem and forms an organ, the *foot*, which absorbs food from the parent plant. Soon after, a swelling, the *apophysis*, appears on the rod-shaped embryo, a little way above its middle. This plays a part in the independent nutrition of the growing sporogonium, being a local assimilatory region composed of cells rich in chloroplasts and provided with abundant intercellular spaces (Fig. 121, *ap.*), whilst the epidermis contains *stomata* resembling those of higher plants.

The upper part of the embryo enlarges progressively to form the spore-producing region, or *capsule*, which, at maturity, is far more conspicuous than the apophysis below it. It becomes raised aloft (Fig. 118, A, C, D) by a considerable elongation of the slender stalk, formed from the region below the apophysis, and this causes rupture of the calyptra. The upper portion of the latter remains for a time as a hood (Fig. 118, A, *ca*), covering the capsule. When this calyptra is removed, the apex of the capsule is seen to be separated from the rest by a slight constriction, and it is this part that becomes detached as a *lid* to allow of the dispersal of the spores.

The internal structure is best studied in a longitudinal section of a nearly ripe capsule (Fig. 121). Here the axis is occupied by a rather broad column of thin-walled parenchyma (*Co.*) passing below into the tissue of the apophysis (*ap.*) and above into that of the lid (*l.*). Surrounding the columella are two concentric cylinders of cells, which are separated by a granular layer of so-called spore mother-cells (*a.*), each of which, by division of its contents, forms four spores within itself. Between this spore-sack and the capsule-wall is a conspicuous air-space (*S.*) bridged by occasional fine threads of green cells. The capsule is protected by a thick-walled epidermis (*ep.*) beneath which are several layers of cells containing chloroplasts. The features just described are equally recognisable in a transverse section through the middle of the capsule.

At maturity all the thin-walled tissues of the capsule shrivel, leaving, apart from the spores, only the epidermis and a dome-shaped group of minute teeth (Fig. 121, *p.*), which arise from a narrow injutting ledge at the lower limit of the lid and project into the latter. Subsequently, when the lid has become detached and blown away by the wind, the aperture of the capsule is occupied by these teeth, which are extremely sensitive to changes in the moisture-content of the air, curling outwards when the latter is dry and inwards when it is damp. In dry weather, therefore, the powdery mass of spores inside the capsule is readily dispersed, whilst in wet weather the dome is reconstituted and the aperture closed.

The spores in most Mosses develop into a branched multicellular filamentous structure, the *protonema*, which exists partly above and partly below ground. The overground portion appears as a green weft on the surface of the soil, and its cells contain numerous discoid chloroplasts, whilst the underground portion closely resembles the rhizoids of the ordinary Moss.

Sooner or later some of the short lateral branches become pear-shaped, and undergo segmentation to form a small Moss-plant. This process takes place at many points on the protonema, and, as the latter usually dies away soon after, the individuals become independent; one Moss-spore may, therefore, give rise to a number of separate plants.

The life-history of the Bryophyta thus includes two distinct phases: the one, concerned in the production of the sexual organs (gametophyte), is relatively highly organised and self-supporting, whilst the other, concerned solely with the production of asexual spores (sporophyte), is always dependent, and relies for its sustenance partly upon food obtained from its host. In the Liverworts in fact, where the sporogonium is not so highly differentiated as in Mosses, it may be altogether parasitic on the sexual phase. The two phases in the life-cycle normally alternate with one another and arise from one another, and a similar alternation is encountered in all the higher groups of plants

CHAPTER XXVI

THE FERNS

APART from Algæ, Fungi, Liverworts, and Mosses, there are several groups of flowerless plants (Cryptogams) which differ from them in the possession of true roots and vascular tissue. These are classed as *Pteridophyta,* or Vascular Cryptogams, and include the Ferns, Horsetails, and Clubmosses. The vascular strands can be readily recognised with a hand-lens in a cross-section of the stem of any common Fern (*e.g.* Bracken, Fig. 122, A).

The Ferns are the only Pteridophyta that are still abundantly represented, the remaining forms being mere relics of groups that once played an exceedingly important part in the vegetation of the world. In most of the common British Ferns the stem is an underground *rhizome* (Fig. 122, B), which is relatively insignificant in comparison with the conspicuous fronds which alone appear above the surface.

These fronds are usually deeply divided (as in the Bracken and Male Fern), but there are some forms in which the blade is almost simple (cf. Fig. 123). The veining is exceedingly characteristic, the midribs of the leaves or leaflets, as the case may be, bearing numerous forked lateral veins which are usually not connected by cross-branches.

The stem rarely shows branching, though this occurs at intervals where the rhizome is elongated (*e.g.* Bracken). In this case, the leaves usually arise in a row, on either side, and are separated by well-marked internodes (Fig. 122, B). In short-stemmed species, however (*e.g.* Male Shield Fern, *Nephrodium filix-mas* [1]), the leaves are densely crowded and show an obvious spiral arrangement. In these more compact forms a conspicuous feature of the rhizome which adds appreciably to its apparent

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[1] Also known as *Aspidium filix-mas* and *Dryopteris filix-mas.*

thickness, are the adhering bases of the leaves, which persist after lamina and petiole have died away (cf. Fig. 122, B). The *roots* usually arise in the neighbourhood of the leaf-bases, and are generally black in colour and forked.

The young *leaf* is mostly more or less densely clothed with brown scaly hairs or *ramenta*, many of which are shed as the blade unfolds; they usually persist, however, upon the petioles (Fig. 123, A, *r.*) and on the leaf-bases clothing the older parts of the stem. As the leaf-rudiment produced behind the growing point gradually develops, the axis of the lamina becomes coiled after the manner of a watch-spring, and, in the case of compound leaves, the individual portions become inrolled in a similar fashion (Fig. 122, C); in this way the growing tips are protected by the older parts. These features are readily observed in a

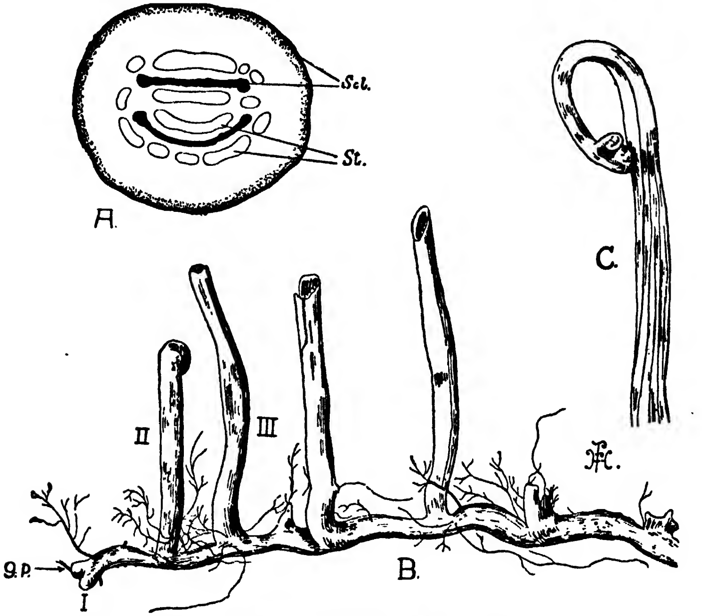

FIG. 122.—The Bracken (*Pteris aquilina*). A, Diagram of transverse section of rhizome. *Scl.*, sclerenchyma; *St.*, vascular strands. B, Rhizome showing apex with growing point (*g.p.*), successively older leaves (I, II, III), and the bases of leaves of former seasons. C, Young frond.

young Bracken-frond, as it emerges from the soil in spring, and the prolonged growth of its tip is evidenced by the retention of the coiled character in the uppermost portion, long after the older basal portion is fully expanded. The development of Fern-leaves is usually very slow, the rudiment being produced and undergoing gradual enlargement for two or more years before the frond appears above the surface (cf. Fig. 122, B, I, II, III).

In the ordinary course of events the Fern-plant sooner or later commences to produce spores. These are developed within small, stalked, usually brown-coloured *sporangia*, almost invariably borne on the under-surfaces of the fronds. Most commonly they are arranged in numerous separate groups, or *sori*, each usually comprising a considerable number of sporangia arising from a slight central swelling of the leaf-tissue known as the *placenta* (Fig. 124, *pl.*).

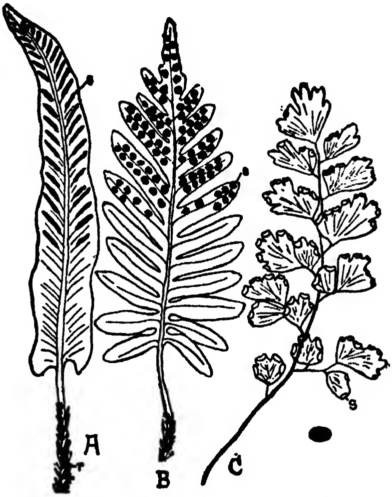

FIG. 123.—Entire fronds of A, Hart's Tongue Fern (*Scolopendrium vulgare*); B, Polypody (*Polypodium vulgare*); and C, Maidenhair Fern (*Adiantum*). *r.*, ramenta; *s.*, sori. (All three considerably reduced.)

Such sori are well seen in the Common Polypody (Fig. 123, B, *s.*) and in the Male Fern (*Nephrodium*). They appear as small brown patches, situated over the side-veins, and in the latter case each is protected by a kidney-shaped outgrowth (*indusium*) of the placenta, which withers when the sporangia are mature.

In the Bracken (*Pteris*) the sporangia form a continuous fringe all round the margin of the leaflet, the incurved edge of the latter functioning as a protective covering.

In transverse sections through a fertile leaflet of *Nephrodium filix-mas* (Fig. 124), the bulging placenta (*pl.*) on the underside is seen to be supplied from the overlying vascular bundle. The indusium (*i*) appears as an umbrella-shaped outgrowth, one layer of cells thick, arising from the top of the placenta. On the sides of the latter are borne numerous sporangia in various stages of development.

A mature *sporangium* (cf. Fig. 124, *a.*) consists of a stalk of elongated cells, terminated by a biconvex *capsule* which is more or less oval in side-view, and encloses the spores within a wall of a single layer of cells. The cells of the wall fit firmly together, and most of them are thin-walled and very flat, appearing more or less polygonal in surface-view, but tabular in optical section. The edge of the capsule, however, is occupied by a single row of specially differentiated cells. The greater part of this band, from the base of the capsule on one side to half-way down the other edge, is composed of cells which have all but their outer walls strongly thickened, and which constitute the *annulus* (*a.* in Fig. 124). The remainder, forming the so-called *stomium*, are much broader and thin-walled throughout and it is here that the mature capsule ruptures.

Each sporangium arises as a papillate outgrowth from a single surface cell of the placenta, which is cut off by a cross-wall, and undergoes further divisions to form stalk and capsule. At a later stage three definite regions can be recognised within the latter, viz. the one-layered capsule-wall, an inner nutritive layer or *tapetum*, and a central cell, the *archesporium*. The last-named divides to form a number of *spore mother-cells*, each of which gives rise to four spores (cf. p. 273). Their development takes place at the expense of the food-materials contained in the granular thin-walled cells of the tapetum, which thus disorganises before the sporangium matures.

With the ripening of the sorus the indusium dries and

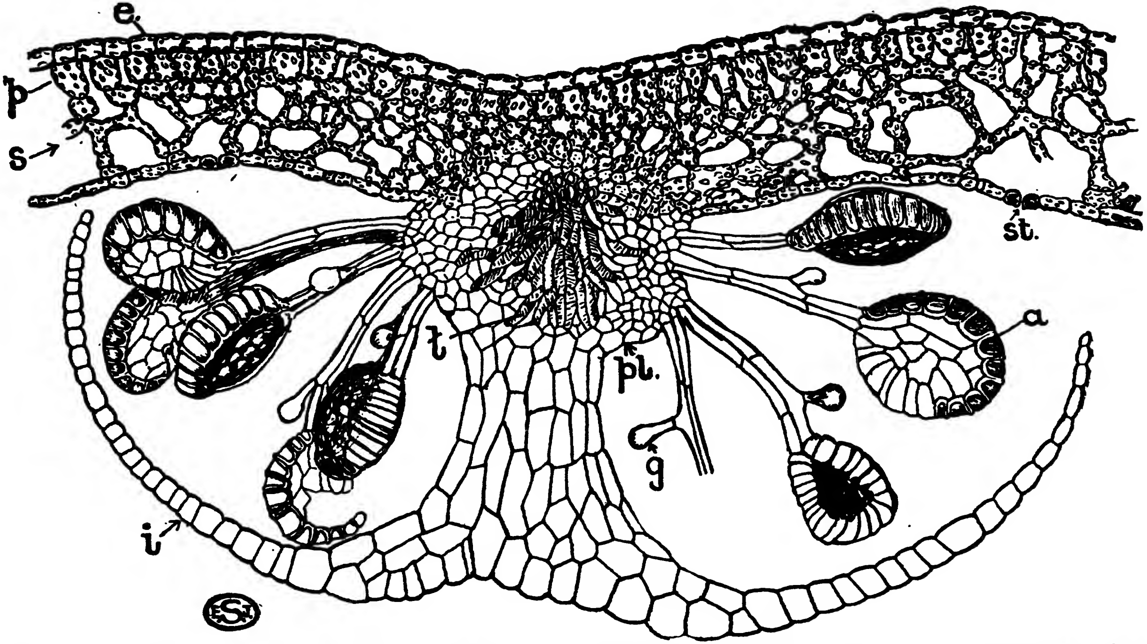

Fig. 124.—Transverse section of leaflet, passing through a sorus, of the Male Fern (*Nephrodium filix-mas*), showing the indusium (*i.*), the placenta (*pl.*), and sporangia in various positions and stages of development. *a.*, annulus; *e.*, epidermis; *g.*, gland on sporangial stalk; *p.*, palisade tissue; *s.*, spongy tissue; *st.*, stoma; *t.*, tracheids.

shrivels, exposing the sporangia, which likewise begin to lose moisture. As evaporation proceeds, the thin outer walls of the annulus commence to bulge inwards (cf. Fig. 124), owing to the gradual reduction in the volume of their sap. Thus an increasing tension is set up in the annulus,[1] which eventually leads to rupture of the capsule-wall along the plane of greatest weakness, viz. the junction between the transversely extended cells of the stomium. On the release of the tension the annulus, carrying with it a great part of the capsule-wall and many of the contained spores, gradually bends back and may even become inverted, but sooner or later there is a sudden recoil and the spores are shot out as from a sling; they are further dispersed by air-currents, and may thus be carried to a considerable distance. The dehiscence of ripe sporangia can be observed under the microscope by adding glycerine.

Apart from the difference of arrangement, to which reference has already been made (p. 266), the sporangia of the Bracken, and most other British Ferns, agree in all essential respects with those of the Male Fern.

In germination the outer coats of the spore are burst, and the innermost is stretched to form a long, colourless, tubular outgrowth, which becomes separated off from the main body of the spore by a transverse wall, and penetrates the soil as the first *rhizoid* of the future plant. The remainder of the spore-contents lengthen into a short horizontal filament whose few cells contain chloroplasts. Within the end-cell two intersecting walls soon arise, and, as a result of further rapid growth mainly in the horizontal plane, a flat, heart-shaped structure is developed. The green plant thus established is known as a *prothallus*, and, when mature, sometimes attains a diameter of over a centimetre (Fig. 125). The central portion (cushion) is several cells thick, but the margins are composed of only one layer. All the cells are alike, and each contains several discoid chloroplasts. From the underside, especially in the region of the cushion, scattered superficial cells grow out as colourless unicellular rhizoids (*r.*), which serve for anchorage and the absorption of moisture.

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[1] It will be realised that the side-walls of the annulus are much less thickened than the horizontal walls, so that the contraction is entirely in the longitudinal direction.

The prothallus is the Fern-plant (*gametophyte*) that bears the sexual organs. These are situated on the underside, and both kinds usually occur on the same prothallus (Fig. 125, ***an.*** and ***ar.***). They are of the same general type as in Mosses, and are produced by the outgrowth of single surface-cells. The male organs, or ***antheridia*** (***an.***), found mainly on the thinner marginal wings and the less robust prothalli, are almost spherical structures (Fig. 126, *g.*), composed of a wall (*w.*) enclosing a small number of relatively large cells (*s*). Each of these mother-cells gives rise, by modification of its protoplast, to a single male cell or spermatozoid which develops as a spirally coiled, spindle-shaped body, bearing numerous cilia near the pointed end (Fig. 126, *d.*). Dehiscence of the antheridium takes place in wet weather by the rupture of the outermost of the three cells constituting its wall

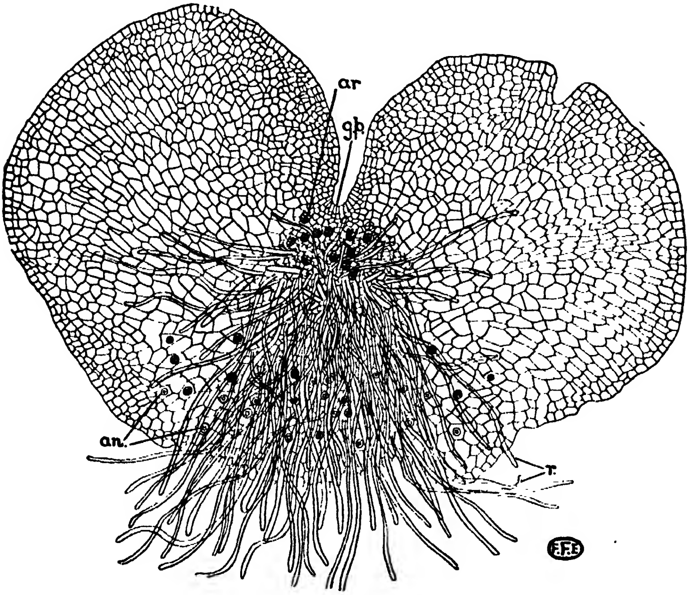

Fig. 125.—Fern-prothallus (magnified about thirty-five times), from the under-surface. A considerable number of antheridia (*an.*) are seen, on the older part, and the projecting necks of twelve archegonia (*ar.*), in the region of the cushion, from which also numerous rhizoids (*r.*) arise. *g.p.*, growing point.

(Fig. 126, *e.* and *f.*) and the naked spermatozoids, escaping from the membranes of the mother-cells, swim in the film of water retained by capillarity between the lower surface of the prothallus and the soil.

The female organs, or *archegonia* (Fig. 125, *ar.*) are restricted to the thicker central region (cushion) and consist of two parts, the swollen venter embedded in the prothallus and the projecting neck (Fig. 126, *a.* and *b.*). The former contains the naked female cell, or egg (*o.*), as well as a small cell situated at the base of the neck (ventral canal cell, *v.c.*). The neck is curved towards the pointed (first-formed) end of the prothallus, and is composed of four longitudinal rows of cells (Fig. 126, *c.*), enclosing a single naked neck-canal cell. At maturity (Fig. 126, *b.*), the four cells at the top of the neck are forced apart by a mucilage containing malic acid, formed from the disorganised neck and ventral canal cells, and an open passage is thus left leading down to the egg. It is apparently the malic acid that attracts the

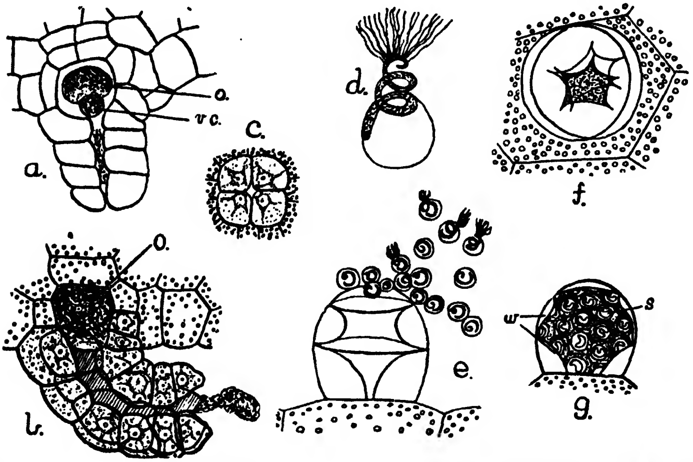

Fig. 126.—*a.*–*c.*, archegonia, *e.*, *f.*, and *g.*, antheridia, and *d.*, single spermatozoid of the Fern. *a.*, immature, and *b.*, mature, archegonium in longitudinal section; *c.*, neck in surface view. *o.*, egg; *v.c.*, ventral canal cell. *g.*, almost mature antheridium in optical section, showing the wall (*w.*) and the spermatozoid mother-cells (*s.*); *e.*, dehiscing antheridium with the escaping spermatozoids; *f.*, dehisced antheridium from above. (*a.* after Goebel; the remainder after Kny.)

spermatozoids to the necks of the archegonia, and sooner or later one of them passes down the neck-canal and penetrates the ovum.

After fertilisation the ovum becomes enveloped by a thin membrane and immediately begins to segment to form an ordinary Fern-plant. The embryo at an early stage develops a large parenchymatous sucker (the *foot*), which becomes firmly lodged in the tissue of the cushion from whose cells it absorbs nourishment. Growth now ensues rapidly, and by degrees, root, stem, and leaf become differentiated. The young Fern, like the sporogonium of Mosses (cf. p. 261), is thus for a time dependent on the prothallus. But, as soon as its root has become established in the soil, and the first green leaf has spread out its lamina to the light, this dependence ceases, and soon after that the prothallus withers away. Several years may elapse, however, before the Fern-plant reaches its mature size.

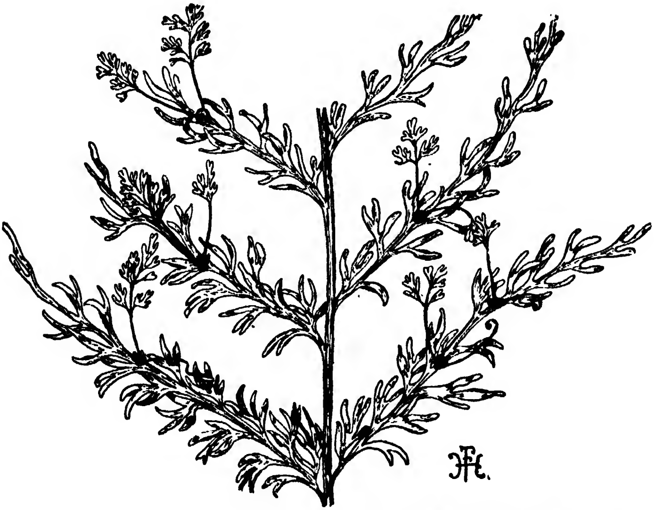

Fig. 127.—Small part of a frond of *Asplenium bulbiferum*, showing the vegetative production of new plants (about half natural size).

It will be recognised that in the life-history of the Fern there are two phases, viz. a leafy, spore-producing plant (*sporophyte*), which usually attains large dimensions, and a sexual generation (*gametophyte*), which is a small and mostly short-lived thallus. The same two reproductive phases are recognisable in the life-cycle of the Moss, where, however, their relative importance is reversed (cf. p. 263). Normally the two generations in the Fern alternate regularly with one another, but occasional abnormalities are encountered.

Thus, in certain Ferns the prothalli may arise by direct budding from the leaves or sporangia, without the formation of spores (*apospory*). In other cases the sporophyte develops vegetatively from the prothallus without the intervention of sexual organs (*apogamy*). Vegetative multiplication of the sporophyte is not infrequent, new plants arising from buds formed on the surface of the fronds, as in the commonly cultivated *Asplenium bulbiferum* (Fig. 127).

In the normal life-cycle, of Mosses and Ferns alike, the spore is the starting-point of the sexual, and the fertilised ovum of the asexual, generation. The spore mother-cells with few exceptions give rise to four spores, after undergoing two successive nuclear divisions. The nuclear changes involved differ, however, in several important respects from those observed in the ordinary vegetative divisions of the plant (cf. p. 75 *et seq.*). At the onset of the first division the chromatin reticulum contracts away from the nuclear membrane and forms a dense mass around the nucleolus (Fig. 128, A), a stage termed *synapsis*.

The first indication that synapsis is ended is the appearance of a number of loops (Fig. 128, A), each formed of two closely approximated chromosomes joined end to end or side by side. The nucleolus has now disappeared, its chromatin material having presumably been absorbed into the chromatin thread. Gradually the whole tangle loosens out, then the loops become shorter and thicker (Fig. 128, B) and break apart ; each segment is composed of the two chromosomes forming one of the loops, now often twisted together (Fig. 128, C). The number of separate portions produced is only *half* that observed in the vegetative divisions of the same plant.

The nuclear spindle is established in the usual way, and the *paired chromosomes* pass on to it (Fig. 128, D) and separate so that *whole* chromosomes from each pair travel to opposite ends of the spindle. Each of the daughter-nuclei thus contains half the number of chromosomes characteristic of the vegetative cells, and, for this reason, this nuclear division is often spoken of as the "*reduction*" division. The second division, in which longitudinal fission of the chromosomes takes place, follows almost immediately, and does not differ essentially from that described for the ordinary vegetative cells.

Each of the four resulting spores (Fig. 128, E) thus possesses half the number of chromosomes found in the spore mother-cell, and so do all the cells of the gametophyte (*haploid phase*). The original number of chromosomes (*diploid phase*) is restored in the fertilised egg after the fusion of the male and female nuclei. It will be realised that the reduction division differs chiefly from the usual type in the occurrence of synapsis and in the passage of *entire* chromosomes to the respective poles of the nuclear spindle. Moreover, there is good reason for believing that each pair of associated chromosomes is made up of the corresponding parts of the paternal and maternal nuclei, so that the material brought together in fertilisation is distributed in reduction (cf. p. 333).

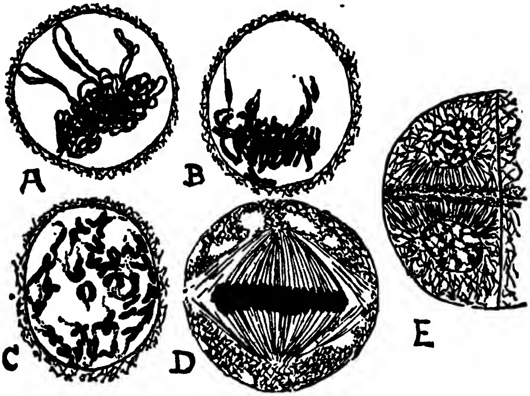

FIG. 128.—Nuclear divisions in spore mother-cells of *Nephrodium* (after Yamanouchi). A, Late synapsis. B, Segmentation of chromosomes. C, Association of chromosomes. D, Equatorial plate. E, Part of a tetrad.

The importance of reduction is also emphasised by its occurrence in animals, although here it usually takes place during the formation of the sexual cells. Reduction occurs in the formation of spores, not only in all Bryophyta and Pteridophyta, but also in the higher plants (Phanerogams). In the Thallophyta the actual reduction has only been observed in relatively few cases, but it cannot be doubted that it takes place in all forms exhibiting a sexual process.

The four nuclei, produced in the spore mother-cell, usually become grouped so as to form a tetrahedral figure. Each, together with part of the cytoplasm, becomes surrounded by a separate wall, the whole of the contents of the mother-cell being thus used up to form four spores (Fig. 128, E). Their faces of contact are more or less flattened and triangular, while the outer walls are convex, so that each spore, at its inception, has the form of a tetrahedron with a rounded base. In many cases, however, the spores round off after the mother-cell membrane has broken down.

In most Ferns there is only one kind of frond which fulfils the ordinary functions of a leaf, as well as those connected with spore-production. In a few species, however, there is division of labour, as in the Hard Fern (*Blechnum spicant*), not uncommon on heaths. Here some of the leaves, spreading out near the surface of the ground, have broad leaflets and are purely vegetative, whilst others, which assume an erect position, have narrow lobes and are almost entirely concerned in the production of sporangia. Such fertile leaves are called *sporophylls.* The division of labour here seen is far more pronounced amongst Flowering Plants, where the production of reproductive organs is delegated to highly specialised leaves forming the flowers.

CHAPTER XXVII

The Flowering Plants (Angiosperms)

The Flowering Plants are the predominant vascular plants on the earth's surface at the present day. Frequent reference has been made to their subdivision into Monocotyledons and Dicotyledons which, apart from differences in the flowers (cf. below), are distinguished by the number of cotyledons in the embryo (p. 31), the anatomical structure of stem (p. 125), root (p. 118), and leaf, etc. The broad outlines of the life-history of a Flowering Plant have already been indicated in Chapter I, but the construction of the flowers and the details of the processes of reproduction require a somewhat fuller consideration.

The flowers, as we have seen, are mostly grouped to form *inflorescences,* in which each flower usually arises in the axil of a modified leaf (*bract,* Fig. 95, p. 208) which serves for its protection while in bud. Two principal types of inflorescences are distinguishable, according to the manner of grouping of the flowers. In the one (known as *racemose* inflorescences, *e.g.* Hyacinth, Shepherd's-purse, Fig. 1) the lowest flower on the main axis is the first and the uppermost the last to open, so that the order of opening is from below upwards or, in the case of flat-topped inflorescences (*e.g.* Hogweed, Carrot), from without inwards. In the other (*cymose* inflorescences, *e.g.* Buttercup, Poppy, Fig. 95) the growth of any given axis of the inflorescence terminates at an early stage with the production of a flower which opens before those on the lateral branches arising below it; hence the order of opening is from above downwards.

The individual flower[1] may be regarded as a compressed shoot, serving for purposes of reproduction and bearing a number of

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[1] The reader is advised to study once more the flower of the Shepherd's-purse (p. 6) before passing on to the subsequent matter.

whorls (cf. p. 47) of specialised leaves, which are usually not separated by internodes. Of these floral organs some are essential for the production of seed (viz. stamens and ovary), whilst others constitute the non-essential *perianth* (viz. the calyx and corolla of the Shepherd's-purse, Fig. 4) which, however, mostly plays an important part in the protection of the flower and in the attraction of insect-visitors.

The expanded end of the peduncle, or flower-stalk, to which the different floral organs are attached is spoken of as the *receptacle*, or *thalamus*. This is frequently more or less convex in form, bearing at its summit the ovary, with stamens and perianth at successively lower levels, as in the Buttercup (Fig. 129, A) and the Tulip (Fig. 130, *r*.) or Lily. Such flowers are said to be *hypogynous*. Occasionally, however, the receptacle is hollowed out, a condition seen in members of the Pea-family (Leguminosæ), and more pronouncedly in the Strawberry and the Rose (cf.

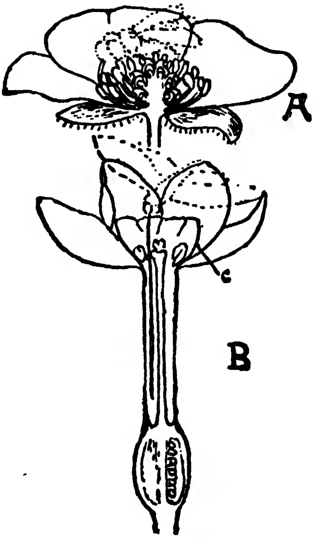

FIG. 129.—Vertical sections of flowers of A, Buttercup (open type); B, Pheasant's-eye Narcissus (tubular type), showing hypogyny and epigyny respectively. The body of the pollinating insect is shown by dotted lines, the proboscis being indicated by a continuous line. *c*, corona.

Fig. 148, p. 310). If the ovary becomes completely enveloped, *i.e.* embedded within the receptacle, so that the remaining floral organs arise from its top, we obtain the kind of flower seen in the Narcissus (Fig. 129, B), Apple (Fig. 148, A), and Hogweed (Fig. 150), which is described as *epigynous*.

In such cases, where the ovary is situated below the other organs, it is described as *inferior* in contrast to the *superior* ovary of the Buttercup, Tulip, Pea, etc.

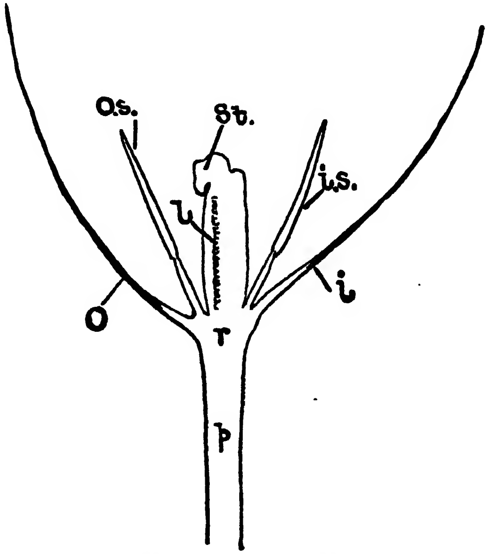

FIG 130.—Longitudinal section of Tulip-flower. *o.*, outer perianth-leaf; *i.*, inner perianth-leaf; *o.s.*, outer stamen; *i.s* inner stamen; *st.*, stigma; *l.*, loculus of ovary showing ovules; *p*, flower-stalk; *r.*, receptacle.

The features just considered are best illustrated by means of *longitudinal sections* through the middle of the flower. In drawing such sections it is advisable to show only the actual cut surface (as in Fig. 130), which is easily done after a little practice, even by those who possess but slight skill in drawing. Such a section should faithfully represent the shape of the receptacle, as well as the order of attachment of the floral organs, and should also indicate the position of the bract with reference to the flower.

Apart from the longitudinal section, a *floral diagram* or ground-plan of the flower is necessary to make its structure quite plain. For this purpose (cf. Figs. 131 and 132) the main axis on which the flower is borne, is shown by a dot and after that the exact position of the different floral whorls, as well as of the bract, with reference to the main axis and to one another, is indicated; all the members arising at one level are placed on the same circle and the ovary is shown in cross-section.

The floral diagram of a Tulip or Lily (Fig. 131) shows that all the different whorls have their parts in threes; this is characteristic of the perianth of Monocotyledons and applies to all the whorls of the flower in the case of the Lily-family (Liliaceæ). On the other hand, in many Dicotyledons (*e.g.* Hogweed, Stitchwort, Primrose), most of the parts are in fives, although in the Buttercup (Fig. 132), for example, this only applies to the calyx and corolla. In some cases, however, the parts of dicotyledonous flowers are in twos or fours (*e.g.* Wallflower, Shepherd's-purse).

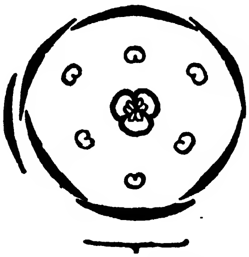

FIG. 131.—Floral diagram of the Lily.

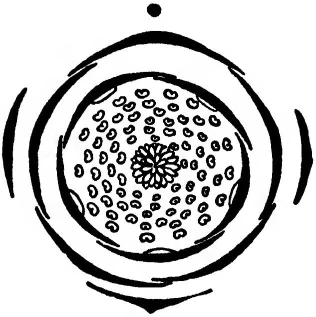

FIG. 132.—Floral diagram of the Buttercup. The two bracteoles are shown on either side of the flower.

A typical flower, both in Monocotyledons and Dicotyledons, has two whorls of perianth-members (cf. Figs. 131, 132). In Monocotyledons (Fig. 131) the main axis lies opposite the interval between two members of the outer whorl, whereas in most Dicotyledons the odd (fifth) member of the outer perianth-whorl is situated opposite the axis (Fig. 132). The Pea-family (Leguminosæ, *e.g.* Sweet-pea, Fig. 149, B) is exceptional in this respect, the odd sepal here being away from the axis. It will be noticed that in general the members of one whorl alternate with those of the next, although this is not without exception.

In Dicotyledons the two whorls of perianth-leaves are usually unlike in appearance, forming the calyx and corolla respectively (cf. Fig. 4). The calyx, comprising the green sepals, has a protective function, as is well seen in most flower-buds in which all the inner parts are completely hidden by it. On the other hand, in many Monocotyledons (Lily, etc.) the two perianth-whorls are quite similar and often highly coloured, like the corolla of Dicotyledons. Such *petals* exhibit a great variety of form in relation to their function as organs of attraction for insect-visitors, to which they often also afford a convenient alighting place (cf. p. 288). In many flowers (*e.g.* Primrose, Narcissus) the sepals and petals are more or less completely joined and often form a long tube at the top of which the limbs of the petals spread out (cf. Fig. 129, B). In other cases (so-called *irregular* flowers) the members of the corolla may differ among one another in form and arrangement, as is well seen in the Pea-family (Leguminosæ). Here the petal nearest the axis is developed as a large upright " standard " ; the two next within form a pair of " wings " on either side of the flower, and these in turn embrace the boat-shaped " keel," which is composed of two petals joined along their lower edges (cf. p. 290 and Fig. 138). In the Dead-nettle again, as in many members of the Labiatæ, the joined corolla is a two-lipped structure, the upper lip shielding the stamens and stigma, and the lower lip forming an alighting platform for pollinating insects.

The *ovary* of the Flowering Plant is composed of one or more structures known as *carpels*, which may either be joined together to form a *syncarpous* ovary (*e.g.* Liliaceæ, Fig. 131) or free from one another, when the ovary is said to be *apocarpous* (Buttercup, Fig. 129, A, Fig. 132). The nature of the carpels is best seen in ovaries of the latter type. Thus, the single carpel composing the young pod of a Pea has the structure of a leaf which is folded round, so that its margins meet. The midrib is marked by a well-defined vascular bundle which lies on the side opposite to that constituted by the junction of the enlarged margins (cf. Fig. 142, *b*.). The latter form the *placentæ* on each of which a row of ovules (cf. p. 7) is borne. The mature pod readily splits both along the midrib and the line of junction of the margins.

The tip of each carpel is produced into a slender outgrowth, the *style*, which terminates in the *stigma*; in syncarpous ovaries the styles are usually likewise joined, but the stigmas commonly remain more or less distinct and indicate the number of component carpels (*e.g.* Tulip, Stitchwort). In many syncarpous ovaries the sides of adjacent carpels are joined together, so that the resulting ovary is divided by partitions or septa into as many compartments, or *loculi*, as there are carpels (*e.g.* three in the Lily, Fig. 131). In other cases the adjacent margins of the carpels are united, without the latter being folded together, the ovary consequently having only one compartment (*e.g.* Violet). The ovules, in all cases, are borne on the edges of the carpels.

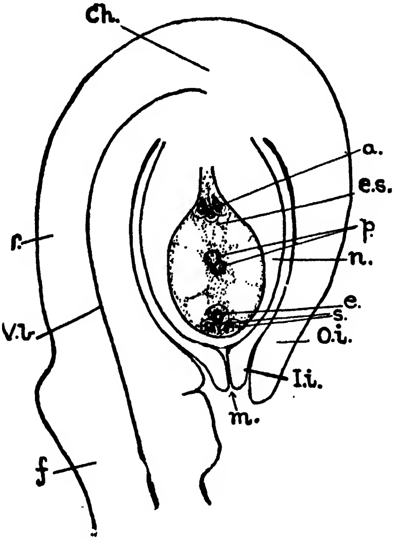

Fig. 133.—Diagrammatic longitudinal section through an anatropous ovule, greatly magnified. *a.*, antipodal cells; *Ch.*, chalaza; *e.*, egg; *e.s.*, embryo sac; *f.*, funicle; *I.i.*, inner integument; *m.*, micropyle; *n.*, nucellus; *O.i.*, outer integument; *p.*, polar nuclei; *r.*, raphe (region of fusion of funicle and outer integument); *s.*, synergidæ; *V.b.*, vascular bundle of raphe.

An ovule (Fig. 133) consists of a stalked parenchymatous body or *nucellus* (*n.*) harbouring a large cell, the *embryo sac* (*e.s.*), and enveloped by two coats or *integuments* (*O.i.* and *I.i.*). The latter arise from the stalk and completely enclose the nucellus except for a narrow opening, the *micropyle* (*m.*) at the far end. By far the commonest type of ovule is that shown in Fig. 133, in which the main body is bent down against its stalk (*funicle, f.*), so that the micropyle (*m.*) is directed towards the placenta. The greater part of the funicle is in this case fused with the adjacent portion of the outer integument, which is in consequence not easily distinguished on this side. The fused region is traversed by the vascular bundle (*V.b.*) which enters the funicle from the placenta, and which extends as far as the base of the nucellus (a region known as the *chalaza, Ch.*).

An ovule invariably arises on the placenta as a small mound of thin-walled cells which represents the future nucellus. Around the base of this the integuments subsequently develop as ring-like upgrowths, the inner being formed before the outer. All ovules are at first erect. The bent form, characteristic of the majority, is due to excessive growth on one side of the rudiment, so that the latter gradually becomes curved till the micropyle points towards the placenta.

Each stamen consists of a stalk or filament and a swollen. pollen-producing part or anther (Fig. 4, A, *a.*). Most commonly the anther is rigidly attached to the filament (*e.g.* Tulip, Fig. 130), but occasionally (as in Grasses, Fig. 137) it is more or less loosely suspended from its end. Stamens, unlike carpels, are usually not joined, although in the Pea-family (Leguminosæ), for example, the stamens cohere by the lower parts of their filaments, which form a tube round the ovary (cf. Fig. 138, C.). More frequently part of the filament is joined to the corolla, so that the stamen appears to arise from the latter (*e.g.* Primrose).

If a cross-section of the anther of a young stamen be examined with a lens, it is possible to distinguish two pairs of cavities, or *pollen-sacs*, one pair situated in each of the two lobes of the anther; the pollen-sacs traverse the full length of the latter and at maturity are filled with pollen. The two anther-lobes are joined together by a middle piece, or *connective*, in which a small vascular strand, continuous with that traversing the filament, is distinguishable (cf. Fig 134, A, *v.b.*), In transverse sections through very young, immature flower-buds, the anthers are seen to consist of uniform thin-walled tissue bounded by a distinct epidermis, whilst a slight lobing foreshadows the future pollen-sacs (Fig. 134, B and C). In transverse sections through older anthers (Fig. 134, A) a mass of pollen mother-cells in the centre of each pollen-sac is seen to be surrounded by a nutritive layer (*tapetum, t.*). This is composed of large, often palisade-like, cells with prominent nuclei and dense contents. Between the tapetum (*t.*) and the epidermis (*ep.*) of the anther are two or more layers, the outermost of which generally consists of rather large, subsequently thickened cells (*fibrous layer, f.*), whilst the others (*m.l.*) are usually very much flattened.

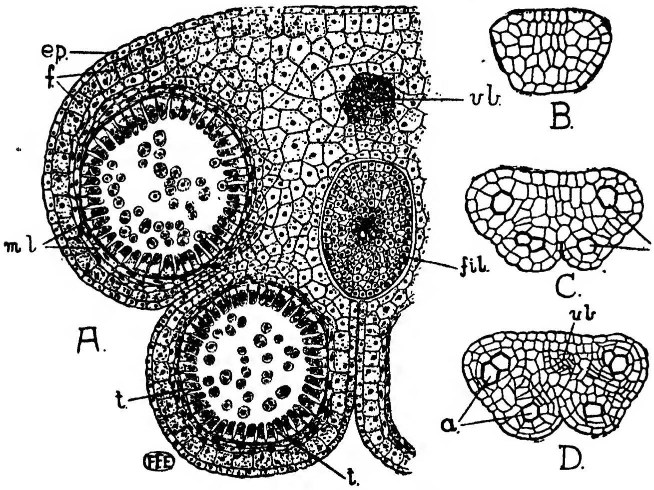

FIG. 134.—Development of the anther. A, Section of rather more than half the anther of a young stamen, showing the pollen-sacs at the mother-cell stage (the mother-cells are seen in various phases of division). B, Section of young anther; C and D, Later stages. *a*, cells dividing to form pollen mother-cells; *ep.*, epidermis of anther; *f.*, fibrous layer; *fil.*, filament; *m.l.*, middle layer; *t.*, tapetum; *v.b.*, vascular bundle of connective. (A original, the remainder after Warming.)

Each pollen mother-cell, as in the case of the spore mother-cells of the Fern, undergoes two divisions (cf. Fig. 134, A), the first of which is the reduction division. The four *pollen grains,* thus formed within each mother-cell, generally fall apart as the membrane of the latter becomes dissolved. During the development of the pollen-grains the tapetum undergoes gradual disorganisation.

The mature pollen-grain possesses a wall of two layers, the outer of which is thick and cuticularised, whilst the inner is delicate. Where the pollen is wind-borne, its surface is commonly smooth, but when conveyed by insects it is usually sculptured in various ways. The outer layer is perforated, or rendered thin, by one or more pores, or pits, through one of which the pollen-tube (cf. p. 292 and Fig. 140, F) emerges on germination.

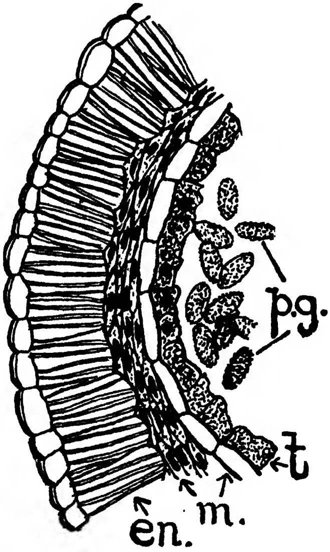

Fig. 135.—Transverse section through part of a pollen-sac of a ripe anther. *en.*, fibrous layer; *m.*, middle layers; *p.g.*, pollen-grains; *t.*, disorganised tapetum.

As the pollen matures the walls of the cells composing the *fibrous layer* become strengthened by radial bars of thickening which are often connected on the inner tangential walls, and simultaneously the cells lose their living contents (Fig. 135, *en.*). At this stage the two pollen-sacs, in each half of the anther, become confluent through the drying up of the intervening thin-walled septa, and it is this same process of desiccation that ultimately leads to the setting free of the pollen. Actual splitting usually takes place longitudinally along the middle line of each anther-lobe. The thickenings of the cells of the fibrous layer (Fig. 135, *en.*) prevent radial contraction, so that the tangential shrinkage brings the bars together like the closing of a fan ; it is the tension thus set up that finally results in rupture.

Before the pollen-grain is shed its nucleus divides into two (Fig. 140, B). One of these becomes surrounded by a small envelope of denser cytoplasm (*generative cell, g.c.*), whilst the other (*tube nucleus, t.n.*) lies freely in the general body of the grain. In this condition the latter is transferred, in one way or another, to the stigma of the same or of a different flower, and here germination takes place.

It can be readily shown that this process of *pollination* is, in most plants, essential for the production of seeds by removing all the stamens from the flowers of an inflorescence, before they have shed their pollen, and then covering the whole with a fine muslin bag to prevent access of foreign pollen. Under these circumstances neither fruits nor seeds ripen, and the same result is obtained in whatever way pollen is prevented from reaching the stigma. Similar experiments have proved that in many plants, though not in all, a larger number of seeds, and frequently more vigorous offspring, are produced if pollination and fertilisation are effected by pollen from the flower of a different individual. When this latter is the case we speak of *cross-pollination*, whereas the term *self-pollination* is used when the pollen comes either from another flower of the same individual or from the stamens of the self-same flower. The advantage of cross- as compared with self-pollination is very apparent in some plants ; for instance, Darwin found that the weight of Cabbages produced from seeds formed as a result of cross-pollination was very much greater than those grown from seeds which had been produced by self-pollination, the former varying between 74 and 130 ounces, the latter between 11½ and 46 ounces.

In view of such facts it is not astonishing that a very large number of plants have developed devices which tend to favour cross-pollination. Most flowers contain both stamens and ovaries—in other words, are *hermaphrodite*, but the two kinds of organs rarely ripen at exactly the same time. In some cases the stamens ripen first (*e.g.* Willow-herb, Fig. 136), whereas in others the stigma matures before the pollen is shed (*e.g.* Figwort). There are, however, all transitions from flowers in which the essential organs ripen almost simultaneously (*e.g.* White Dead-nettle) to flowers in which the one kind of organ has withered before the other is mature (*e.g.* Rose-bay Willow-herb, Fig. 136, Figwort). In all such extreme cases self-pollination is obviously prevented in the earlier stages of flowering, although a considerable number of these plants make provision for self-pollination just before fading. Still greater certainty of cross-pollination is ensured when stamens and ovaries occur in distinct flowers (*e.g.* Hazel, Birch) or even on separate individuals (Stinging Nettle).

Fig. 136.—Flowers of Rose-bay Willow-herb, to illustrate ripening of stamens and stigma at different times (natural size). In the upper flower the stamens are alone mature; in the lower one they have withered, whilst the four stigmatic lobes are now spread out. *St.*, stigma; ♂, male stage; ♀, female stage.

The conveyance of pollen from the stamens to the stigma can be effected by various agencies, the commonest being wind and insects. In the former case it is evident that pollination depends largely on chance, and therefore, if it is to be successful, a much greater amount of pollen must be produced than is necessary to effect fertilisation. We find, indeed, that wind-pollinated plants either have numerous stamens in their flowers (*e.g.* Poplar, Elm), or relatively large anthers producing copious pollen (*e.g.* Grasses, Fig. 137). Moreover, the stigma is frequently richly branched and feathery (*e.g.* Grasses, Fig. 137), so that pollen is the more easily caught.

It is further of advantage that the pollen of wind-pollinated plants should be readily shaken out of the flowers by the wind; and we may relate to this the frequent occurrence of loose hanging inflorescences (*e.g.* Birch, Hazel), or of anthers which are loosely hinged on long projecting filaments, so that they are moved by the least puff of wind (Grasses, Fig. 137). The pollen itself is dry and powdery in character, and usually has a smooth surface, so that there is no tendency for the grains to cling together, thus facilitating a wider distribution.

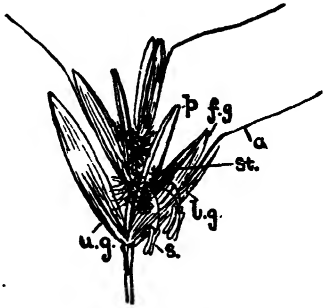

FIG. 137.—Group of flowers of the Wild Oat, forming a small spike. *s.*, stamen; *St.*, stigma; *f.g.*, *l.g.*, *p.*, and *u.g.*, different bracts of the inflorescence; *a.*, bristle-like outgrowth.

The flowers of wind-pollinated plants are usually green and inconspicuous (*e.g.* Dog's Mercury, Ash). They naturally lack all those attractive mechanisms which are so marked a characteristic of insect-pollinated flowers.

Such flowers are visited by insects either for their nectar or pollen and are usually very conspicuous. Nectar is the most frequent attraction and is produced in special glands called *nectaries* (cf. p. 135) which may be situated on almost any protected part of the flower, generally near its base, and often on the floral receptacle (cf. Fig. 150, *n.*). Many members of the Lily-family (*e.g.* Tulip) develop nectaries in the wall of the ovary, these appearing as narrow slits when the latter is cut across. In the Buttercup a nectary is situated at the bottom of each petal, protected by a small flap, whilst in the Pea-family the nectar is formed on the bases of the stamens. In some flowers (*e.g.* Violet, Larkspur) the nectar accumulates in a special tube-like outgrowth of the perianth, known as a spur, whereby it becomes accessible only to long-tongued insects.

Not all insect-pollinated flowers, however, produce nectar, a limited number (*e.g.* Poppy) providing no other bait than pollen. It may be added that, even in flowers having nectaries, insects generally take a certain amount of the pollen as food. In addition to nectaries and pollen the colours and odours of flowers constitute important means of attraction.

Since, provided they are visited, pollination is almost a certainty in insect-visited flowers, particularly those frequented by Bees and Humble-bees, a much greater economy in pollen can be effected than in wind-pollinated plants. As a consequence there is usually (except in flowers visited for pollen only) a relatively small number of stamens, a feature which becomes the more marked the more perfect the mechanism for pollination. The pollen itself generally has a rough or sticky coat, so that it readily adheres to the insect's body, whilst the stigma is not as richly branched as in most wind-pollinated forms, but has a very sticky receptive surface.

The chief pollinating insects are Bees, Butterflies, Moths, Flies, and Beetles. The Honey Bee and other Hymenoptera are most important, but Diptera play a large part in the pollination of some flowers (*e.g.* Blackberry). All pollinating insects, except Beetles, possess a special sucking organ, the tongue, or *proboscis*, arising from the under side of the head, very short in Flies and exceptionally long in Butterflies and Moths, where it is coiled up when not in use. Flowers possessing a long, narrow, corolla tube (Fig. 129, B) are not accessible for nectar to any but long-tongued insects, whilst wide-open flowers (Fig. 129, A) provide nectar for a variety of visitors, both with long and short probosces.

In the majority of cases the insect actually alights on the corolla, or perianth. The position taken up depends largely on the situation of the nectary and the form of the perianth, and varies greatly in different plants, though usually constant for the same kind of flower. As a result, very diverse parts of the body (viz. proboscis, head, back, or abdomen) may become dusted with pollen, and it is of importance in this connection that these are often covered with hairs to which the pollen readily adheres. Sooner or later the stamens and stigma in any given flower come to occupy similar situations, so that the pollen taken from the anthers of one flower will be likely to get rubbed against the stigma of another.

The simplest kinds of mechanism for pollination are seen in regular flowers in which the perianth is symmetrically developed (*e.g.* Lily, Tulip, Buttercup). In flowers with a wide-open, shallow corolla (*e.g.* Buttercup, Stitchwort) almost any insect-visitor can obtain honey, and such are often sought out by small insects which may in their erratic wanderings effect pollination, although no doubt it is often only pollen from the same flower that is transferred. Flowers possessed of a perianth-tube (*e.g.* Narcissus, Primrose), on the other hand, can only be visited by insects with a long proboscis, and the variety of these becomes the more restricted the greater the length of the tube. The most perfect mechanisms are found in flowers with an irregular corolla,

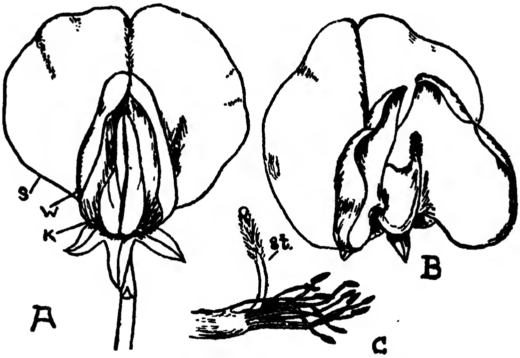

FIG. 138.—Pollination and flower-structure in the Sweet Pea (natural size, C enlarged). A, Flower of Sweet-pea, seen from the front. B, Ditto with stigma and stylar brush emerging, as during pollination. C, Essential organs enlarged, showing position when released from keel. *k*, keel; *s*, standard; *st.*, style; *w*, wings.

a device which usually results in a very marked restriction of insect-visitors. In such flowers the honey is usually well concealed, and to obtain it the insect is compelled to take up a definite position with reference to the essential organs, so that only the more intelligent Bees and Humble-bees are usually successful.

A good illustration is afforded by the irregular flowers characteristic of the Pea-family (Leguminosæ), whose corolla has already been described on p. 280. The essential organs in these flowers are completely enclosed within the keel (Fig. 138, *k*), and are thus efficiently protected; they consist of ten stamens (Fig. 138, C), often of two lengths, the filaments forming a tube around the central pod-like ovary, which is provided with a long style (*St.*) ending in a stigma of varied character. Honey is usually produced on the inner sides of the bases of the filaments and accumulates in the trough formed by them. In most cases the stamen nearest the axis is free (cf. Fig. 149, B), thus leaving a cleft in the stamen-tube for the insertion of the proboscis of an insect.

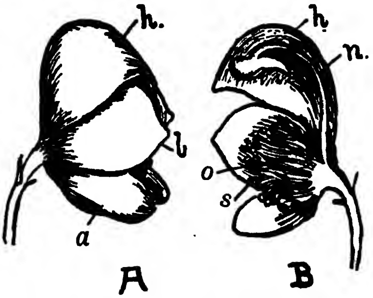

Fig. 139.—Flowers of the Monkshood (natural size). A, Entire flower seen from the side. B, Halved flower. *a*, front perianth-member; *h.*, hood; *l.*, lateral member; *n.*, nectary; *o.*, ovary; *s.*, stamens.

The upright standard (*s*) constitutes the most conspicuous feature of the flower, whilst the wings (*w.*) form the alighting platform, the head of the insect being directed towards the standard. Since obviously neither nectar nor pollen is easily reached, these flowers can only be visited with profit by sufficiently intelligent insects and by such as are heavy enough to weigh down the keel and expose the essential organs; Bees fulfil both requirements, and are indeed amongst the commonest visitors. The base of each wing is provided with an outgrowth which fits into a hollow in the adjacent petal of the keel (Fig. 138, B) and thus, when a Bee alights on the wings, these and the keel get depressed simultaneously. As a result the essential organs are exposed and rub against the *under surface* of the insect's body. If the latter already bears pollen from another flower it will effect cross-pollination at the same moment as it rubs against the stigma. When it flies away, the parts of the flower return to their original positions and the keel again screens the essential organs.

In the Dead-nettle, and Labiatæ generally, it is the back of the insect which receives the pollen from the stamens beneath the upper lip (cf. p. 280). The honey is at the base of the corolla-tube and, therefore, only accessible to insects such as have a body sufficiently large to fill the space between the two lips. Still another type is illustrated by the Monkshood (Fig. 139), where the insects alight on the front (*a*) and side (*l.*) members of the perianth and probe for the honey which is secreted in two long-stalked nectaries (*n.*) beneath the hood (*h.*). In the first (male) stage of the flower the underside of the Humble-bee becomes covered with pollen, whilst subsequently, in the female stage, when the stamens have curled right back, it is the stigmas that touch the Bee's abdomen.

CHAPTER XXVIII

THE FLOWERING PLANTS (*continued*)

AFTER the pollen-grain has been carried to the stigma it puts out a thread-like pollen-tube, which grows down the style till it reaches the cavity of the ovary. The tube nucleus passes into the tip of the growing pollen-tube, and the naked generative cell sooner or later follows suit (Fig. 140, C), the latter ultimately producing two male nuclei (cf. below). The pollen-tube traverses the cavity of the ovary and thus reaches the micropyle of one of the ovules.

The downward growth of the pollen-tube is mainly determined by a chemical stimulus due to substances contained in the ovules or in the ovary-wall. This fact can be experimentally demonstrated by sowing pollen-grains of the Wild Hyacinth (*Scilla*) in a 5 per cent., or of *Echeveria retusa* in a 15 per cent., solution of cane-sugar around a fragment of the ovary, taking care to avoid the inclusion of air-bubbles. Observed under the microscope, the pollen-tubes tend to grow in the direction of the piece of ovary.

Returning to the ovule, we may recall that the nucellus contains a large cell, the embryo sac (cf. p. 282), which appears usually before the integuments have become plainly differentiated and during the development of which a reduction division occurs.

Until it has reached a considerable size the embryo sac contains but a single nucleus, which usually lies in the middle of a strand of cytoplasm running from end to end of the sac and bridging the large central vacuole. Sooner or later, however, a nuclear division occurs, and the two resulting nuclei wander towards opposite ends of the embryo sac, where each again divides twice. Three of the four nuclei thus formed, at the end remote from the micropyle, usually become separated by cell-walls and constitute the *antipodal cells* (Figs. 133 and 140, D, *a.*) which probably assist in the nourishment of the young embryo.

Of the four nuclei at the micropylar end of the embryo sac, three become surrounded by an envelope of specialised cytoplasm, and constitute a group of naked cells known as the *egg-apparatus* (Fig. 133). This consists of the *egg* (*e.*) and two *synergids* (*s.*), the latter, which usually lie in front of the former, being supposed to aid in the passage of the male nucleus to the female cell. The remaining nuclei (one at each end, one of them the sister-nucleus of the egg) pass back to the middle of the embryo sac, where these two *polar nuclei* (Figs. 133, *p.*; 140, D, *p.n.*) meet and ultimately fuse to form the *primary endosperm nucleus*. This is the stage reached by the embryo sac at the time of fertilisation.

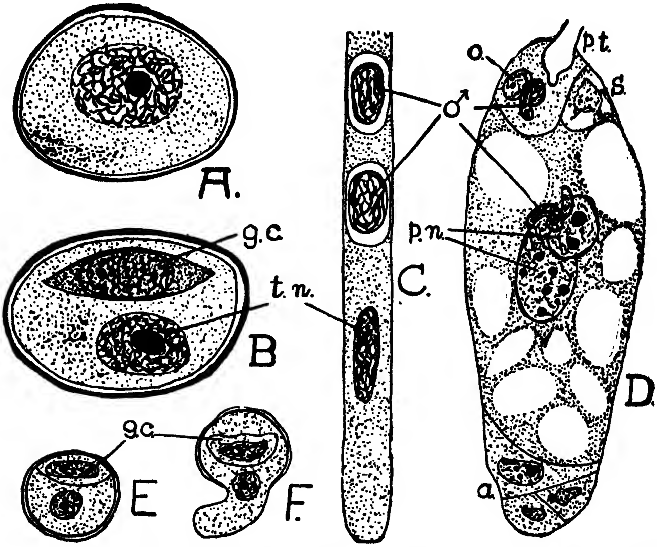

FIG. 140.—Germination of pollen and fertilisation. A–D, Lily (*Lilium*) (after Guignard). E–F, Tulip (*Tulipa*) (after Ernst). A, Mature pollen-grain, showing the single nucleus. B and E, Later stage, showing generative cell (*g.c.*) and tube nucleus (*t.n.*). C, Tip of pollen-tube with tube nucleus (*t.n.*) and two male cells (♂). D, Embryo sac at the moment of fertilisation, showing antipodals (*a.*), polar nuclei (*p.n.*), ovum (*o.*), one synergid (*s.*), and the two worm-shaped male cells (♂) discharged from the tip of the pollen-tube (*p.t.*). F, Early stage in formation of pollen-tube.

Having passed through the micropyle, the pollen-tube penetrates the overlying nucellus, and thus reaches the embryo sac. Meanwhile the generative cell has divided to form two *male nuclei* (Fig. 140, C ♂), which are extruded from the tip of the pollen-tube, and, entering the embryo sac, fuse respectively[1] (*a*) with the egg, and (*b*) with the two polar nuclei (cf. Fig. 140, D), or with the nucleus formed by the fusion of the latter. The former fusion results, in the usual way, in the production of an embryo, whilst the product of the second divides repeatedly, so that the sac becomes occupied by a continuous thin-walled tissue, the *endosperm*, which stores food for the developing embryo.

During the nuclear divisions leading to endosperm-formation, the fertilised egg, now provided with a cell-wall, enlarges considerably and commences to segment. The first division is unequal, a smaller cell situated at the end away from the micropyle being cut off from the large remaining portion. The latter (Fig. 141, I–VI, *b*) plays no further part in the development of the embryo. The smaller segment undergoes successive transverse divisions, so as to give rise to a short elongating thread, the *suspensor* (Fig. 141, *S*). Hereby the slightly larger hemispherical terminal cell (*e*), which subsequently produces the embryo proper, is carried down into the heart of the developing endosperm. Young *proembryos* at this stage of development, with a suspensor composed of a number of flat cells, are readily squeezed out of very young seeds of the Shepherd's-purse, such as can be removed from the ovaries of flowers which have not yet faded; the seeds are best mounted in water, and gentle pressure applied by tapping the cover-glass. More advanced stages can be obtained in the same way from progressively older seeds. These show rather longer suspensors and an increasing number of divisions in the enlarging embryonal cell (Fig. 141, IV–VI).

By degrees the embryo assumes a more or less flattened form, and, at its wider free end, the future *cotyledons* appear as two lobes (VII, *Co.*) between which the *plumule* (*p*) develops. The attached end of the embryo invariably becomes the *radicle* (VIII, *r*), which thus faces towards the micropyle (cf. p. 25). Such embryos are to be found in seeds from almost ripe fruits

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[1] This process is often spoken of as "double fertilisation."

(cf. IX). In Monocotyledons the single cotyledon arises at the apex of the embryo and the plumule towards one side.

In all cases the embryo only attains to a certain, though varying, stage of development and then enters upon a resting period, securely shielded within the testa until conditions arise suitable for germination (p. 22). This dormant stage, passed within the seed, is a feature distinguishing the higher forms of plants from Ferns, Mosses, etc. The embryo may absorb all the food-materials in the endosperm before entering upon its resting-stage (*exalbuminous* seeds, as in the Shepherd's-purse, Pea, etc.), or

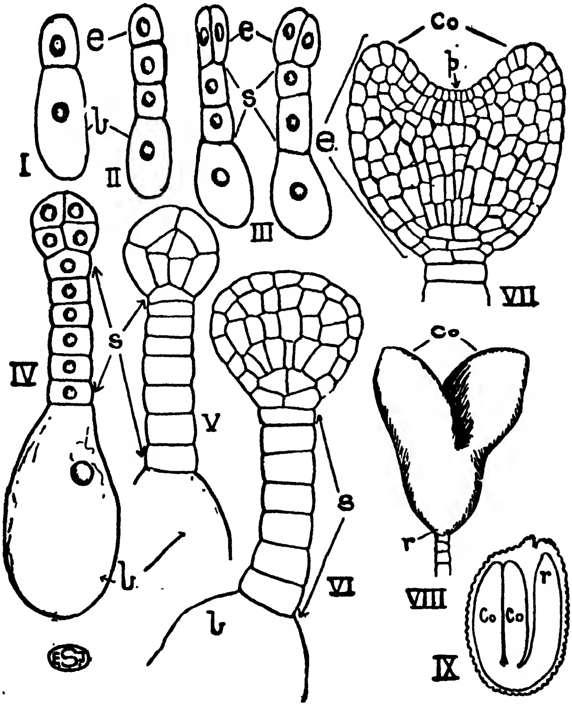

FIG. 141.—Embryology of the Shepherd's-purse (*Capsella bursa-pastoris*) The successive stages are numbered I–IX. In VII and VIII only the embryo and a small part of the adjacent suspensor are shown. IX is a longitudinal section of a mature seed, showing the coiled embryo. *b*, basal cell; *Co.*, cotyledons; *e*, embryo; *p*, plumule; *r*, radicle; *S*, suspensor.

part of the endosperm may persist up to the time of germination (*albuminous* seeds, *e.g.* Castor Oil, most Monocotyledons).

Exceptions to the normal sequence of events described in the foregoing pages are by no means uncommon. *Apogamy* (cf. p. 273), for example, has been recorded in quite a large number of Compositæ (*e.g.* Dandelion). In such cases the reduction division does not appear to occur, and the embryo arises from an unfertilised cell of the embryo sac having the normal number of chromosomes. Such apogamy is of course akin to vegetative propagation, but gains the advantages afforded by the mechanism for seed-dispersal (cf. below). Despite the non-occurrence of a sexual process in such apogamous forms, pollination sometimes appears to furnish a necessary stimulus for embryo-formation. More rarely it is an ordinary cell of the nucellus that divides to form the embryo (*e.g.* Orange, *Citrus*), a case analogous to the *apospory* described among Ferns (p. 273).

The stimulating effect of fertilisation is not confined to the embryo, but also affects the ovule as a whole and the enveloping ovary, whilst in some cases even adjacent parts of the flower undergo considerable enlargement and change (*e.g.* the receptacle in the Strawberry). The seeds are often many times the size of the ovules from which they sprang (*e.g.* Pea, Bean, etc.). The enlarged ovary-walls become the fruit-wall or *pericarp*, and the hardened integuments form the *testa* of the seed, upon which the micropyle remains recognisable in most cases (cf. p. 23). The fruit thus corresponds to the whole ripened ovary, whilst the seeds are the matured ovules contained within it. In many plants the calyx persists as a protection around the fruit, after the rest of the flower has withered (*e.g.* Campion, Snapdragon, etc., Fig. 142, *e*, *f*).

There are two principal types of fruits, viz. the dry and the fleshy. Among dry fruits two kinds can again be distinguished, the one usually remaining attached to the parent-plant and splitting open to liberate the contained seeds (dehiscent fruits), whilst in the other the pericarp merely decays away after the fruits reach the ground (indehiscent fruits). Practically all indehiscent fruits are one-seeded, whilst many-seeded ones are dehiscent. The necessity for dehiscence in the latter class is obvious, since otherwise all the seeds would come to germinate at the same spot and the offspring would harm one another by mutual competition.

Examples of dry indehiscent fruits are furnished by the *achenes* with a membranous, and the *nuts* with a hard, woody pericarp. The fruit of the Buttercup (Fig. 142, *a*) consists of a collection of achenes, each derived from one carpel of the apocarpous ovary, whilst the Hazel and the Acorn provide instances of nuts. It may be mentioned, however, that some of the nuts of commerce (*e.g.* Walnut, see p. 298) are not nuts in the botanical sense.

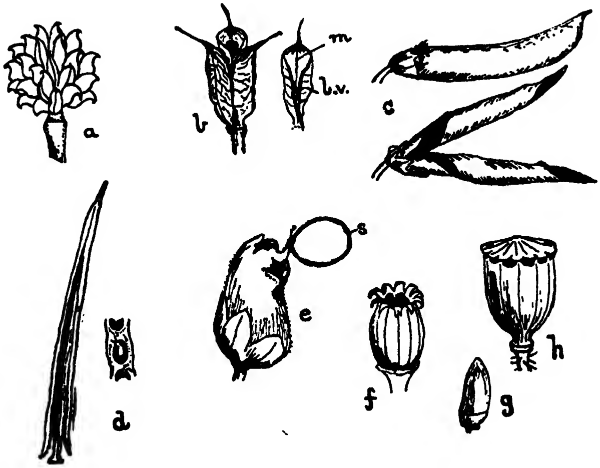

Fig. 142.—Examples of dry fruits (*a* and *d* natural size, *g* somewhat enlarged ; others slightly reduced). *a*, Buttercup (collection of achenes). *b*, Monkshood (three follicles). *m*, midrib of carpel ; *l.v.*, lateral vein of same. *c*, Tare (legume) ; lower figure shows pod after dehiscence. *d*, Wallflower (siliqua) ; right-hand figure shows portion of septum with seeds. *e*, Snapdragon (capsule with apical pores). *s*, style. *f*, Campion (capsule with teeth). *g*, Plantain (capsule with lid). *h*, Poppy (porous capsule).

Examples of the dehiscent type of dry fruit are furnished by the pod (*legume*) of the Pea-family (Leguminosæ), which consists of a single carpel and splits along both margins (Fig. 142, *c*) and the various kinds of *capsules* (Fig. 142, *e*-*g*). The latter are illustrated by the Lily, where dehiscence takes place by three longitudinal slits, and by the Poppy (Fig. 142, *h*) and Snapdragon (Fig. 142, *e*), where the capsule opens by small pores in the pericarp.

The two principal types of *fleshy fruits*, both indehiscent, are the *berry* and the *drupe*. The former has a pericarp which is fleshy throughout (Fig. 143, B and D), whilst in the latter the inner part (endocarp) is hard and stony (Fig. 143, F, *en.*). Examples of berries are furnished by the Currant, Gooseberry (Fig. 143, A-B), Bittersweet (Fig. 143, C-D), and Tomato. The Date is a single-seeded berry in which the hard stone is constituted by the endosperm, the actual testa forming the delicate membrane around the latter. Other special kinds of berries are seen in the Orange, Lemon, Grape, Banana, Cucumber, and Vegetable Marrow.

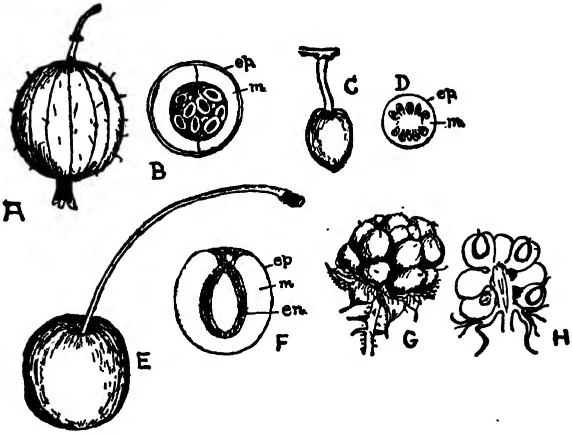

FIG. 143.—Types of fleshy fruits (slightly reduced). A–B, Gooseberry, entire and in cross-section. C–D, Bittersweet (berry), entire and in cross-section. E–F, Cherry (drupe), entire and in longitudinal section. G–H, Blackberry (collection of drupes), entire and in longitudinal section. *en.*, endocarp ; *ep.*, epicarp ; *m.*, mesocarp.

Typical drupes are illustrated by the Plum, Cherry (Fig. 143, E-F), Almond, Peach, etc., whilst the Walnut and Coco-nut are drupes in which, however, the layers outside the endocarp are generally removed before they are placed on the market. The Raspberry and Blackberry (Fig. 143, G and H), which are derived from apocarpous ovaries, furnish instances of compound fruits composed of small drupes.

In some cases the fleshy, edible part of the fruit is derived entirely from parts other than the ovary. Thus, in the Strawberry, the true fruits consist of a number of minute achenes, which are carried up on the surface of the much enlarged and fleshy receptacle, whilst in the Apple and Pear the edible part is likewise formed by the receptacle which here completely envelopes the inferior ovary (the core; cf. Fig. 148, A). The fruit of the Fig is a deeply hollowed inflorescence axis bearing the true fruits (the so-called "seeds") within.

Far more important than an enumeration of the characters of fruits is the relation which these bear to the dispersal of the seeds. Nearly all plants produce far more seeds than can ultimately survive, the bulk of the seedlings being killed off as the result of competition with more successful ones. Since, however, plants of the same kind require similar food and conditions of growth, the struggle will be keenest between individuals of the same species; this can be observed in any seed-bed that has been too densely planted, whereas one sown with mixed seeds will support a considerably greater number of individuals. Moreover, a large proportion of the seeds shed by a plant will be carried to situations unsuitable for a further development, *i.e.* they will not germinate. In view of this great mortality it is of advantage that a plant should produce numerous seeds and that these should be widely scattered, since in this way some are certain to find a suitable situation and the risk of competition with the parent or with one another is overcome. Most plants, in fact, utilise wind or animals for the better dispersal of their seeds or fruits.

A very simple type of mechanism for *wind-dispersal* consists in the production of minute and light seeds (*e.g.* Foxglove). Not uncommonly an expansion of the pericarp in the shape of a *wing* helps in the distribution of one-seeded fruits, good instances being afforded by the Ash (Fig. 144, A) and the Elm. Similarly in the Sycamore (Fig. 144, B) and Maple the fruit splits at maturity into two winged achenes. Winged seeds are rarer in the British flora, but are found, for instance, in the Honesty and Scotch Fir.

In many cases the pericarp or testa is produced into hairs, so that we obtain *plumed* fruits and seeds. Good examples of the latter are seen in the Willow and Willow-herb (Fig. 144, D), both of which have capsules. In the Old Man's Beard, a common climber in hedges (Fig. 144, F), the style of each achene is feathery and enlarges after fertilisation to form a plume. A peculiar type of plumed fruit is found in the Dandelion-family (Compositæ), where a number of fine hairs (the *pappus*) arise from the top of the inferior ovary and form a kind of parachute by means of which the achenes drift readily in the air (Fig. 144, E).

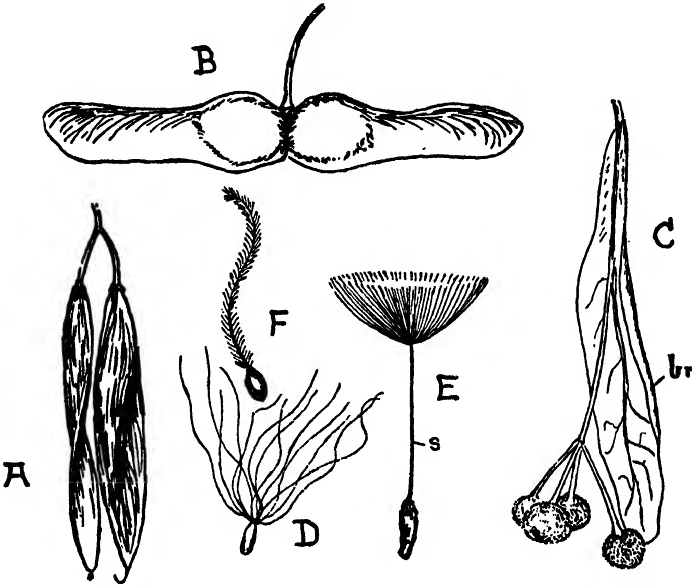

Fig. 144.—Winged and plumed fruits and seeds (all natural size). A, Ash (two winged achenes). B, Sycamore (splitting into two winged achenes). C, Lime. *br.*, bract. D, Plumed seed of Willow-herb. E, Dandelion (achene with superior pappus). *s*, stalk. F, Old Man's Beard or Clematis (achene with feathery style).

It has been noticed that a number of fruits have a succulent pericarp (Fig. 143), amongst them being many of those which are commonly eaten. These depend for dispersal on animals and, as adaptations to this end, we can recognise the usual bright colouring, the fleshy edible character of part or whole of the pericarp, and the fact that in all these fruits the seed-contents are protected by a hard covering (the testa in the case of berries). As a consequence of the last feature, such seeds are able to pass through the digestive tracts of animals without the embryo coming to harm, the seed being deposited with the fæces; thus a certain amount of manure is available for the seedling which subsequently develops. Some of these seeds indeed will only germinate after they have been subjected to the action of the digestive juices within the animal's body. Even when the stone is not swallowed, the bird or other animal generally carries the fruits some little distance from the parent before dropping the seeds. In the Mistletoe part of the flesh of the fruit is very sticky, so that the contained seed adheres to the bill of the bird, who rubs it off on to the branch of a tree; the seedling is thus from the first attached to the plant on which it lives (p. 176).

A considerable number of low-growing herbs develop hooks on their fruits or on adjacent parts of the flowers, and such *burr-fruits* are usually distributed by hairy animals. Examples are furnished by the Goosegrass (*Galium aparine*), Burdock (*Arctium*), and Herb Bennett (*Geum*, cf. Fig. 159).

The possession of a good dispersal mechanism is generally one of the characteristics of so-called weeds. Many of the Compositæ (Dandelion, Groundsel), the Willow-herb, Goosegrass, etc., belong to this category. Such plants are usually among the first to establish themselves on newly exposed soil.

CHAPTER XXIX

THE CLASSIFICATION OF PLANTS

THE Flowering Plants are classed as Angiosperms, and constitute one subdivision of the Phanerogamia (Spermaphyta), the highest group of the Vegetable Kingdom. The other subdivision, the Gymnosperms, includes as its chief representatives the Conifers (*e.g.* Larch, Yew, Scotch Fir). These are all either trees or shrubs, which are mostly evergreen, with leathery, needle-shaped leaves (Fig. 145). A typical example is afforded by the Scotch Fir (*Pinus sylvestris*). This, like many other Conifers (*e.g.* Cedar, Larch), possesses short shoots (cf. Figs. 145, 146) arising in the axils of scale-leaves (Fig. 146, *s.l.*) and bearing the needle-like foliage leaves in pairs (Fig. 146, *d.s.*), long shoots being usually produced only at the beginning of each season's growth. In the Yew (*Taxus baccata*), however, the leaves are borne directly on the long shoots.

The reproductive organs are produced in so-called *cones* which are of two kinds, male and female, both occurring on the same plant in the Scotch Fir, but on distinct plants in the Yew. In the Scotch Fir the male cones are evident towards the end of May as conspicuous yellow clusters composed of small egg-shaped structures, each of which takes the place of a short shoot (Fig. 145 ♂) and represents a single male cone. These cones consist of a central axis bearing numerous leaf-like organs, to the under side of which a pair of large pollen sacs is attached (Fig. 146, D, *p.s.*). The male cones of the Yew arise in the axils of the foliage leaves.

The copious pollen is carried by the wind to the female cones, which in the Scotch Fir appear as small reddish bodies, about one-third of an inch in length, borne just beneath the terminal bud of the newly formed shoot (Fig. 146, A, upper part). The central axis of the female cone bears numerous paired structures, the lower member of each pair (Fig. 146, B, *L.S.*) being small and scale-like, whilst the other, which is relatively large and thick, (*U.S.*) carries two small ovules (*O.*) on its upper surface. The ovules resemble those of Angiosperms, but possess only a single integument and have the micropyle directed towards the axis of the cone; at maturity the embryo sac contains a continuous tissue (prothallus) developing miniature archegonia at the end nearest the micropyle. Some of the pollen is blown between the scales of the female cone and is sucked down on to the nucellus of the ovule, where it puts out a pollen-tube which conveys the male cells to the archegonia.

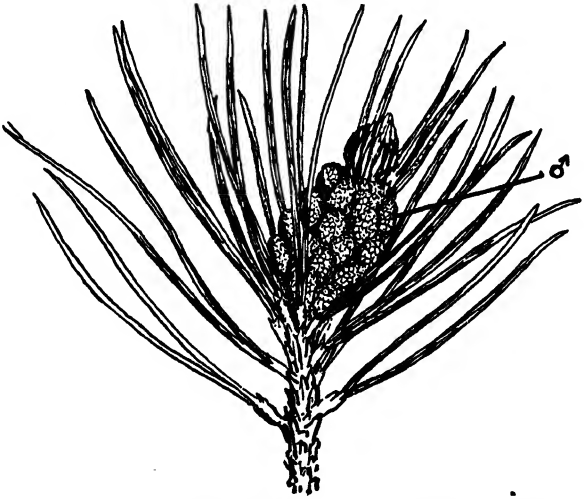

Fig. 145.—Portion of a branch of the Scotch Fir, bearing a cluster of male cones (♂) on the lower part of the year's growth (natural size). Near the top of the latter are seen, closely crowded, a number of immature short shoots.

The actual process of fertilisation is deferred until the subsequent season so that, during the summer, cones of two ages are to be found on a Scotch Fir (Fig. 146, A), viz. those just pollinated (the upper in the figure), and others just fertilised (the lower one in Fig. 146, A), but pollinated in the late spring of the previous year. The latter shed their seeds in the autumn, the empty brown cones, with widely separated scales, often remaining attached to the parent-tree for some time. The winged seeds are albuminous (cf. p. 27), and are peculiar in having an embryo with numerous epigeal cotyledons (Fig. 146, C), the method of germination being very much like that of the Castor Oil. The female cones of the Yew are bud-like in appearance and contain but a single ovule which, after fertilisation becomes enclosed in a bright red fleshy cup.

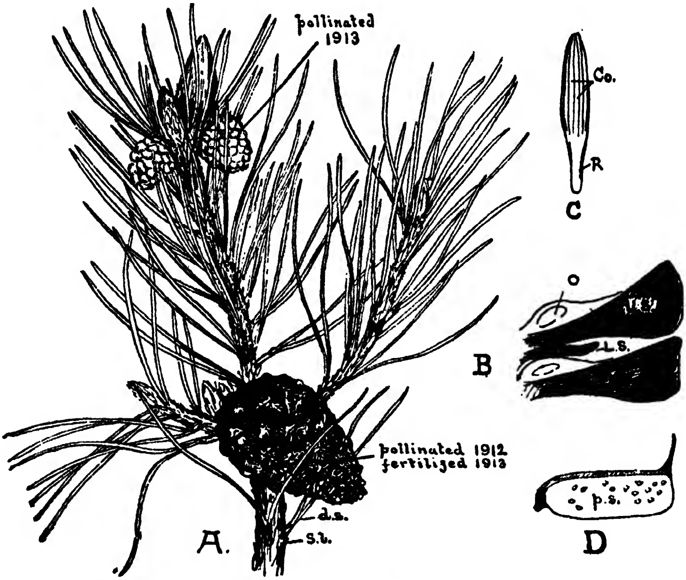

FIG. 146.—The Scotch Fir. A, Branch bearing female cones of two ages (about one-half natural size). *d.s.*, short shoot; *s.l.*, scale-leaf. B, Scales and ovules from a young female cone, cut through lengthwise (much enlarged). *L.S.*, lower scale; *O*, ovule; *U.S.*, upper scale. C, Embryo, dissected out of a ripe seed (enlarged). *Co.*, cotyledons; *R*, radicle. D, Single stamen from a male cone, in longitudinal section, showing one of the large pollen sacs (*p.s.*) (much enlarged).

It will be noticed that the chief difference between the Gymnosperm and the Angiosperm lies in the fact that the ovules of the former are not enclosed in an ovary, with the result that the pollen is brought direct to the ovule instead of being received on a stigma. Moreover, the wood of the Gymnosperm is composed entirely of fibre-like tracheids (cf. p. 144), and there are other distinctions that are beyond the scope of this book.

Now that the entire Vegetable Kingdom has been surveyed, it will be useful to give the following résumé of its principal subdivisions:—

I. Cryptogamia (Flowerless Plants).

- 1. Thallophyta (plant-body unicellular or a thallus, simple sexual organs).
  - Flagellata (an artificial assemblage of simple organisms related to Algæ, Fungi, and Protozoa).
  - Algæ (*Sphaerella*, *Spirogyra*, Seaweeds, etc.).
  - Charales (Stoneworts).
  - Myxomycetes (Slime Fungi).
  - Bacteria.
  - Fungi.
    - (*a*) Phycomycetes (*e.g.* *Mucor*, *Pythium*).
    - (*b*) Basidiomycetes (*e.g.* Rusts, Toadstools, Puffballs).
    - (*c*) Ascomycetes (*e.g.* *Peziza*, *Penicillium*).
    - (*d*) Lichenes.

- 2. Archegoniatæ (female organ an archegonium).
  - Bryophyta (*e.g.* Liverworts, Mosses; without roots or true vascular tissue; sexual phase in the life-history predominant).
  - Pteridophyta (with roots and true vascular tissue, asexual phase in the life-history predominant).
    - Filicales (Ferns).
    - Equisetales (Horsetails).
    - Lycopodiales (Club-mosses).
    - And other groups, mainly known as fossils.

II. Phanerogamia or Spermaphyta (Seed Plants).

- 1. Gymnospermæ (with naked seeds, including Conifers and Cycads).
- 2. Angiospermæ (with protected seeds, the Flowering Plants proper).
  - (*a*) Monocotyledons (including Liliaceæ, Gramineæ, Palms, etc.).

(*b*) Dicotyledons.

1. Polypetalæ (petals of corolla free, *e.g.* Ranunculaceæ, Cruciferæ, Leguminosæ, Rosaceæ, Umbelliferæ).
2. Sympetalæ (petals of corolla joined, *e.g.* Solanaceæ, Scrophulariaceæ, Labiatæ, Compositæ).

It is apparent that, starting with simple forms like many of the Algæ, composed of but a single cell or of a mere thread of cells, we first pass to more elaborate types like the Liverworts and Mosses; from these we come to vascular plants, such as the Pteridophyta, till we reach the culmination of complexity in the Flowering Plants. These groups, however, include many thousands of different species, and in order to provide an oversight of this immense diversity a classification is necessary; moreover, since plants are classed on the basis of all their characteristics, classification aims at placing similar plants near together and dissimilar ones more or less far apart, so that it affords an expression of the relationships between the different forms. We therefore group plants into various aggregates resembling one another in an increasingly greater number of features.

Thus, certain forms are classed together as ***species*** (*e.g.* the different forms of Shepherd's-purse, cf. Fig. 3), the individuals differing only in minute details, such as shape of leaves, presence or absence of hairs, time of flowering, etc. Different species are grouped together in a wider aggregate, the ***genus***, as for example the diverse kinds of Buttercups; all the species of such a genus resemble one another in certain important characters, but differ in more numerous and more appreciable respects than the individuals of the same species. For instance, in the case of the Buttercups, all the species agree in having flowers with a calyx and corolla, nectary-bearing petals, numerous stamens, a fruit composed of a collection of achenes, etc. The individual species, on the other hand, differ in habit, in the shape and degree of lobing of the leaves, the size and colour of the petals, the form of the flower-stalk, and the character of the pericarp, as well as in many other small points. The Buttercups, together with other genera such as the Clematis, Anemone, Marsh Marigold, Christmas Rose, Columbine, Monkshood, Larkspur, etc., are comprised in the *family* or *natural order* Ranunculaceæ, all of them being distinguished by possessing leaves with sheathing bases, a hypogynous flower, numerous stamens, an apocarpous ovary, and fruits frequently consisting of achenes. On the whole, reproductive characters are of greater importance in distinguishing genera than the vegetative organs which serve more particularly to identify species, since the features of the organs of reproduction are more constant among related forms.

All the species of a given genus are in scientific usage designated by a common Latin name, all the Buttercups, for instance, being described as species of the genus *Ranunculus.* The species are distinguished by a second Latin word placed after that denoting genus; thus, the Meadow Buttercup is known as *Ranunculus acris*, whilst the Field Buttercup is *Ranunculus arvensis.* In the summary of families given below the Latin name of each genus is placed in brackets after it.

The members of any one group therefore resemble one another in numerous features, and it is reasonable to suppose that these have, at some period more or less remote, been derived from a common ancestor. In this way, by studying the various groups of plants and classifying them according to their apparent resemblances, we get an approximate estimate of their relationships. Evidence is thus obtained for the belief that the first plants to flourish on the earth were simple forms like the Algæ, and that from such, in the course of the ages, there have gradually arisen more and more complex forms until ultimately the Flowering Plants were evolved. A study of the remains of plants preserved as fossils supports this view, since it shows that the Angiosperms did not appear on the surface of the earth till a relatively late epoch, the flora of earlier ages (*e.g.* the Coal Measure period) consisting largely of Fern-like plants and Gymnosperms (cf. also p. 335). The earliest plants known, viz. those of the Devonian rocks, are of very simple construction.

A brief enumeration of the chief characters of some important families of British Flowering Plants is appended, and serves to illustrate the features upon which such grouping is based.

A. DICOTYLEDONS[1]

(a) POLYPETALOUS FAMILIES

1. RANUNCULACEÆ

Mostly perennial herbs with alt. (except *Clematis*) leaves, often deeply lobed and having sheathing bases. Flrs. mostly reg. (irreg. in Larkspur, Monkshood), ☿, hypog., all parts free, commonly with A ∞ G ∞ (Fig. 132). Perianth either consists of K and C (Buttercup, Fig. 132) or of one or more petaloid (*i.e.* coloured) whorls ; sta. mostly spiral ; ov. apocarp., sup. Nectaries of various shapes, between sta. and perianth. Fruit a collection of separate carpels, either one-seeded and indehiscent (achenes, Fig. 142, *a*), or several-seeded and dehiscent (follicles, Fig. 142, *b*). An acrid juice (sometimes poisonous) often present.

The family includes : Monkshood (*Aconitum*), with irreg. flrs. and reduced petals, two of which form nectaries beneath the hood (Fig. 139) ; the Anemones (*Anemone*) ; Columbine (*Aquilegia*) ; Marsh Marigold (*Caltha*), marsh-plant ; the Old Man's Beard (*Clematis*), a woody climber with opp. leaves and feathery styles (Fig. 144, F) ; Larkspur (*Delphinium*), irreg. flr. having a single projection or spur into which two nectary-bearing processes from the petals project ; Hellebore and Christmas Rose (*Helleborous*), with a persistent perianth-whorl, often green, and trumpet-shaped nectaries ; the Buttercups (*Ranunculus*, Fig. 129, A), with a number of aquatic sp. (Water Crowfoots), usually with white flrs.

Cimicifuga and *Hydrastis*, whose roots are employed medicinally, also belong to this Family. The Nutmeg (*Myristica*), Camphor Tree (*Cinnamomum*), and *Sassafras* belong to closely allied groups.

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[1] In describing the following families we shall frequently employ a *floral formula* to indicate the usual number of parts in the successive whorls. The number of members in each is represented by a numeral and, where there is more than one whorl of the same kind, the numbers for each are joined by a + sign. The calyx is represented by K, the corolla by C, a perianth by P, the stamens by A, and the ovary by G. The joining together of members of a whorl is indicated by putting the corresponding numeral in brackets, whilst a line above or below the numeral representing the ovary marks the inferior or superior position of the latter. Apart from this, the following abbreviations are employed : *alt.*, alternate ; *apocarp.*, apocarpous ; C, corolla ; *cpd.*, compound ; *cpl.*, carpel ; *epig.*, epigynous ; *flr.*, flower ; *hypog.*, hypogynous ; *inf.*, inferior ; *infl.*, inflorescence ; *irreg.*, irregular ; K, calyx ; *opp.*, opposite ; *ov.*, ovary ; *plac.*, placenta ; *reg.*, regular ; *sp.*, species ; *sta.*, stamen ; *sup.*, superior ; *syncarp.*, syncarpous ; *unisex.*, unisexual ; ♂, male ; ♀, female ; ☿, hermaphrodite ; ∞, numerous.

2. CRUCIFERÆ

Annual or perennial herbs with alt. leaves devoid of stipules, often bearing branched hairs; leaves simple or more or less lobed (Fig. 3), often forming rosettes. Infl. without bracts, a raceme (p. 276). Flrs. usually white or yellow, reg., ☿, hypog., all parts except cpls. free, usually with K2+2 C4 A2+4 $G\underline{(^2)}$ (Fig. 147). Petals often clawed and alternating with the four sepals; sta. 2 short and 4 long ones; ov. syncarp., bicarp., with a partition, ovules arising from walls (Fig. 147), resulting in a pod-like fruit (siliqua, Fig. 142, *d*) dehiscing from below upwards, the seeds remaining attached to the partition. Non-poisonous and rich in sulphur-compounds.

The following are common British genera: Charlock (*Brassica*), including Cabbage, Cauliflower, Kohl-rabi, Mustard, Turnip, Brussels Sprout; Shepherd's-purse (*Capsella*), a weed with short triangular fruits; Wallflower (*Cheiranthus*); Scurvy Grass (*Cochlearia*), maritime, often with succulent leaves, the Horse Radish being a sp. of this genus; Cress (*Lepidium*), with slimy seeds; Stock, (*Matthiola*); Water-cress (*Nasturtium*); Radish (*Raphanus*), with a constricted siliqua breaking up into one-seeded segments; Jack-by-the-Hedge or Hedge-Mustard (*Sisymbrium*), with leaves tasting of garlic.

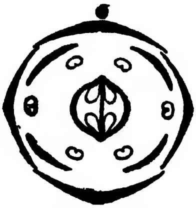

FIG. 147.—Floral diagram of Cruciferæ (Wallflower).

In the allied Papaveraceæ, to which the Opium Poppy belongs the stamens are generally numerous and latex is present,

3. ROSACEÆ

Perennial herbs, shrubs, or trees, with alternate leaves, often having stipules, and simple or compound. Flrs. reg., mostly ☿, with a more or less hollow receptacle (Fig. 148) or epig., all parts generally free, usually with K5 C5 A5+5+5+ . . . $G\infty$. Ov. usually apocarp. and sup. (syncarp and inf. in Apple, Pear, etc., Fig. 148, A). Honey formed on receptacle between sta. and cpls. Fruit various, a drupe, an aggregate of drupes or achenes, etc.

The following are common British genera: Hawthorn (*Cratægus*), with stem-spines (p. 165); Strawberry (*Fragaria*), with runners and fleshy receptacle (p. 299); Herb Bennett (*Geum*), with hooked achenes (Fig. 159); Almond, Apricot, Cherry, Plum, Sloe (*Prunus*), with drupes (Fig. 143, E–F); Apple, Pear, Medlar, and Mountain Ash (*Pyrus*) (Fig. 148, A); Rose (*Rosa*), a scrambler, with a fruit largely composed of the deeply hollowed receptacle (Fig. 148, B); Blackberry, Raspberry, Bramble (*Rubus*), scramblers, with fruit consisting of a number of drupes (Fig. 143, G–H).

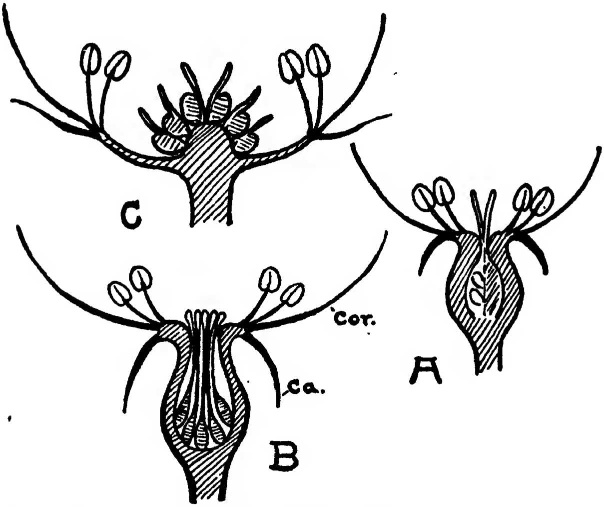

FIG. 148.—Diagrammatic longitudinal sections of flowers of the Rosaceæ. *A*, Apple; *B*, Rose; *C*, Cinquefoil; *ca.*, calyx; *cor.*, corolla. In each figure the receptacle is shaded.

4. LEGUMINOSÆ

Annual or perennial herbs, shrubs, or trees, alt. leaves with stipules and usually cpd., leaflets entire, frequently modified into tendrils (p. 212); roots with root-tubercles (p. 255 and Fig. 117). Infl. racemose. Flrs. irreg., ☿, usually with K(5) C5 A(5 + 5) G1 (Fig. 149). K more or less joined, frequently two-lipped; for further structure of flr., see pp. 280 and 290, and Fig. 138. Fruit a legume (Fig. 142, *c*). Many are common meadow-plants.

The commoner genera are: Broom, Laburnum (*Cytisus*), all 10 sta. joined; Everlasting Pea, Sweet Pea (*Lathyrus*), Fig. 138, with terminal part of leaf modified to tendrils, large stipules, and winged stems and petioles; Medick (*Medicago*), with heads of small flrs. and spirally coiled legumes; Runner Bean (*Phaseolus*); Pea (*Pisum*); Clover (*Trifolium*), with flrs. in heads and trifoliate leaves; Furze or Gorse (*Ulex*), a spiny plant (Fig. 79, B) characteristic of heaths and commons, with explosive fruits; Tare or Vetch, Broad Bean (*Vicia*), with leaves often ending in tendrils.

Amongst the foreign forms are *Mimosa* and *Acacia* in which the flrs. are regular. Several are important medicinally. Thus, Senna is the product of species of *Cassia*, and the root of *Glycyrrhiza* is obtained from the plant of that name. Several gums are yielded by *Astragalus* spp.

5. Umbelliferæ

Mostly perennial herbs, with large, alt., usually cpd. leaves without stipules and having big sheathing bases; stem hollow and often ribbed; a prominent tap-root generally present. Infl. with all the flrs. on the same level, and arising close together from the top of the stem, the outer opening first (umbel). Flrs. small, usually white or yellow, reg., ☿, epig., all parts except cpls. free, almost invariably with K5 C5 A5 G(2) (Fig. 150). K very small and inconspicuous; petals often distant from one another; ov. inf., biloc., with 1 ovule in each compartment; stigma bilobed. Nectary a swelling on top of ov. (Fig. 150). Fruit splitting at maturity into two one-seeded portions. All parts of the plant usually contain aromatic oils, often of commercial value (*e.g.* Angelica, Aniseed, Caraway, etc.).

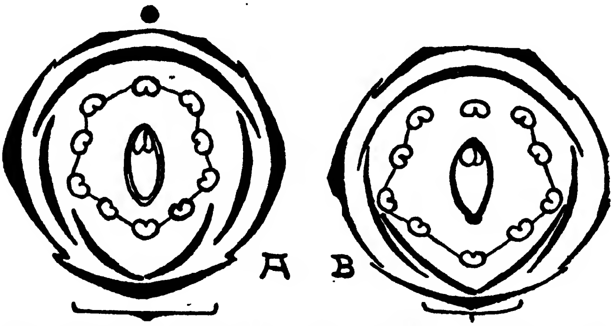

Fig. 149.—Floral diagrams of Leguminosæ. *A*, Needle Furze; *B*, Sweet Pea.

The following are familiar members: *Angelica*, used as a sweetmeat; Caraway, Parsley (*Carum*); Carrot (*Daucus*), with a tuberous root and spiny fruits; Fennel (*Fœniculum*), used in flavouring; Hogweed (*Heracleum*) (Fig. 150), a hedge-plant with huge umbels;

Water Dropwort (*Œnanthe*), a marsh- or water-plant with swollen stems; Parsnip (*Peucedanum*) with a tuberous root.

The following are very poisonous: Fool's Parsley (*Aethusa*), a garden-weed; Wild Celery (*Apium*), the form used as a vegetable having been rendered harmless under cultivation; Water Hemlock (*Cicuta*), a marsh-plant; Hemlock (*Conium*).

Asafœtida (*Ferula*) and Aniseed (*Pimpinella anisum*) also belong here.

(*b*) GAMOPETALOUS FAMILIES

1. Labiatæ

Annual or perennial herbs, with opp., often hairy leaves; square hollow stems, swollen at the nodes. Flrs. in axillary clusters, irreg., ☿, hypog., usually with K(5) C(5) A4 $G\underline{(2)}$ (Fig. 151). K joined, generally with 5 prominent teeth; C 2-lipped, petals joined; sta. 2 long and 2 short, the one nearest the axis missing; ov. sup., bicarp., but 4 loc. owing to division of each of the two loculi, each loculus with 1 ovule; stigma bilobed. Honey produced round base of ov. Fruit splitting into four achenes, protected by persistent K. Leaves often with glandular hairs (p. 135) forming aromatic oils (*e.g.* Lavender, Rosemary, Marjoram).

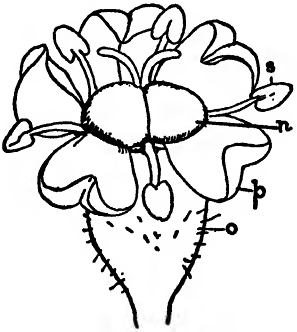

Fig. 150.—Single flower of the Hogweed (considerably enlarged). *n*, disc (nectary); *o*, ovary; *p*, petal; *s*, stamen.

The British genera include: Bugle (*Ajuga*), a woodland-plant with a small upper lip; Dead-nettle (*Lamium*), common weeds; Horehound (*Marrubium*), a plant with a bitter taste; Mint (*Mentha*), aromatic herbs, frequently found in marshes; Ground Ivy (*Nepeta*); Sage (*Salvia*), with only 2 sta.; Thyme (*Thymus*), on heaths, aromatic, with an almost reg. corolla.

2. SOLANACEÆ

Closely allied to Scrophulariaceæ, from which they are chiefly distinguished by their reg. flrs. Annual or perennial herbs, or shrubs, occasionally climbers (*e.g.* Bittersweet, *Solanum dulcamara*), with alt. or opp. leaves. Flrs. generally reg., ☿, hypog., generally with K(5) C(5) A(5) G($\underline{2}$). Sta. occasionally dehiscing by apical slits (*e.g. Solanum*). Plane of symmetry of ov. is usually oblique to the plane of symmetry of the flr., instead of coinciding with it as in Scrophulariaceæ. Fruit a capsule or berry. Many poisonous members, some used medicinally (*e.g.* the genera marked *).

Important genera are: Deadly Nightshade (*Atropa* *), with a berry; *Capsicum* *, whose fruits furnish red pepper; Thorn-apple (*Datura* *, Fig. 49), with a spiny, capsular fruit; Henbane (*Hyoscyamus* *), flrs. yellow veined with purple, with a capsule dehiscing by a lid; Tobacco (*Nicotiana*); Potato, Tomato (*Solanum*).

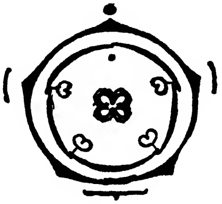

FIG. 151.—Floral diagram of Labiatæ (Dead-nettle). The missing stamen is indicated by a dot.

3. SCROPHULARIACEÆ

Annual or perennial herbs, with alt. or opp., often hairy leaves without stipules, frequently with square stems. Flrs. usually irreg., ☿, hypog., generally with K(5) C(5) A4 G($\underline{2}$). K joined, mostly irreg.; C various; sta. usually 2 long and 2 short; ov. sup., bicarp., biloc. with swollen placs. bearing ∞ ovules; stigma bilobed. Honey formed beneath the ov. Fruit a capsule. Many poisonous.

Common British genera are: Snapdragon (*Antirrhinum*); Foxglove (*Digitalis*), a woodland-plant, with alt. leaves and irreg. tubular corolla, used medicinally, poisonous; Figwort (*Scrophularia*), hedge- or marsh-plants, with 1 barren and 4 fertile sta.; Mulleins (*Verbascum*), mostly hedge-plants, with alt. leaves, 5 sta. with very hairy filaments, and almost reg. flrs.

4. COMPOSITÆ

Annual or perennial herbs, with usually alt. leaves without stipules, often hairy. Infl. a dense head (capitulum) of small flrs. or florets

(Fig. 152, A), the latter often of two kinds, the outer strap-shaped (ray-florets) and the inner tubular (disc-florets), but sometimes all strap-shaped or all tubular; the whole head enveloped by a protective covering of bracts. Flrs frequently yellow, reg. or irreg., ☿ or unisex. (especially the ray-florets), epig., usually with $K_0\, C(5)\, A(5)\, G(\overline{2})$ (Fig. 152, G). K usually absent or represented by hairs (*pappus*); petals joined to form a tube or a strap-shaped structure (Fig. 152, B and C); sta. joined by their anthers; ov. inf., uniloc., bicarp., with 1 ovule; stigma bilobed. Nectary ring-shaped round base of style. As the flrs. mature the style gradually grows up through the anther-tube, pushing the pollen in front of it (Fig. 152, C–E). Fruit an achene surmounted by the pappus (p. 300). A considerable number are common weeds.

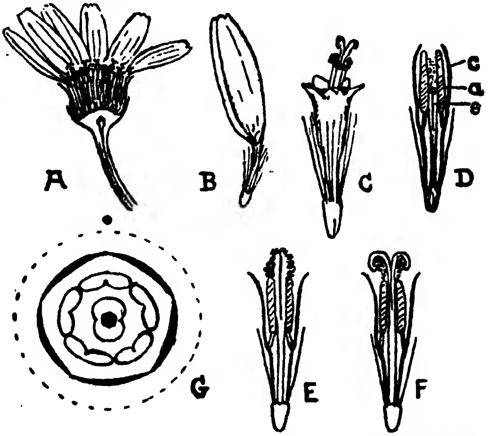

Fig. 152.—Floral structure and pollination in the Marsh Ragwort (A, natural size, other figures somewhat enlarged). A, Capitulum in longitudinal section. B, Ray-floret. C, Disc-floret with style protruding from anther-tube. D, Ditto, in longitudinal section, at an earlier stage. E, Ditto, with style just emerging. F, Ditto, late stage. G, Floral diagram of disc-floret.

The family includes: Leopard's Bane (*Arnica*), used medicinally; Mugwort, Absinth, Wormwood (*Artemisia*),[1] maritime or hedge-plants, very hairy; Michaelmas Daisy (*Aster*); Daisy (*Bellis*), a common weed of lawns and pastures; Thistles (*Carduus*, *Cnicus*),[1] with spiny leaves and purple or white flrs., often weeds; Chicory (*Cichorium*),[2] common weed with blue flrs.; Dog-daisy (*Chrysanthemum*), a

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[1] All florets tubular.

[2] All florets strap-shaped; latex present.

meadow-plant; Elecampane (*Inula*); Lettuce (*Lactuca*)[2]; Chamomile (*Matricaria*), common cornfield-weeds; Groundsel, Ragwort (*Senecio*), common weeds; Sow-thistle (*Sonchus*),[2] cornfield-weeds; Tansy (*Tanacetum*),[1] used medicinally; Dandelion (*Taraxacum*),[2] common weed with tuberous root; Coltsfoot (*Tussilago*), common weed, with solitary capitulum appearing very early, before the leaves, and having unisex. flrs. only; Salsify (*Tragopogon*),[2] with tuberous root, narrow grass-like leaves, and long bracts.

The following Compositæ are often cultivated: Artichoke and Cardoon (*Cynara*), young capitula of former used as a vegetable; *Dahlia*, with tuberous roots; Sunflower, Jerusalem Artichoke (*Helianthus*); *Scorzonera*, a vegetable, with tuberous root.

B. MONOCOTYLEDONS

1. LILIACEÆ

Perennial herbs, with underground rhizomes or bulbs, and sheathing lanceolate leaves. Infl. commonly a raceme. Flrs. reg., ☿, hypog., generally with $P3 + 3\,A3 + 3\,G^{\underline{(3)}}$ (Fig. 131). P generally petaloid, free or joined; sta. occasionally joined to the petals; ov. sup., usually containing ovules. Honey often formed in ovary wall (p. 287). Fruit a berry or capsule. Many early-flowering.

Common British forms are: Onion, Garlic (*Allium*); *Asparagus*, the young shoots being used as a vegetable; Meadow Saffron (*Colchicum*), poisonous, meadow-plant, with a corm and a very long corolla-tube, flrs. in autumn, fruits in spring when the leaves appear; Lily of the Valley (*Convallaria*), poisonous; Lily (*Lilium*); Solomon's Seal (*Polygonatum*), woodland plant with a joined perianth; Wild Hyacinth (*Scilla*), in woods; Tulip (*Tulipa*), poisonous. Foreign members of the group yield Squill (*Urginea*), Sarsaparilla (*Smilax ornata*), and Aloes (*Aloe* spp.).

2. GRAMINEÆ

Annual or perennial herbs, with alt. leaves in two rows having narrow blades and long sheathing split bases; nodes swollen; stems hollow and jointed. Unit of infl. a *spikelet* (Fig. 137), *i.e.* a small group of 1–5 sessile flrs. borne on a very short axis, with a pair of bracts (*glumes*, Fig. 137, *l.g.* and *u.g.*) at the base, which more or less enclose the flrs.; spikelets arranged in cpd. inflrs. Individual flrs. arising in axils of bracts (termed *flowering glumes*, Fig. 137, *f.g.*), the tips of which often form long bristles or *awns* (*a*); very low down on the stalk each flr. bears a two-keeled structure (the *pale*, Fig. 137,

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[1] All florets tubular. [2] All florets strap-shaped; latex present.

p); the parts of the flr. till mature completely hidden between flowering glume and pale. Flrs. reg., ☿, hypog., generally with A3 $G\underline{(^1)}$. Between the sta. and the flowering glume two small green fleshy outgrowths, the *lodicules*, perhaps representing members of a reduced perianth. Sta. with long filaments and large, loosely hinged anthers (Fig. 137). Ov. sup., monocarp., with 1 ovule; stigma two-lobed and feathery (Fig. 137). Fruit an achene.

Common British genera are: Sweet Vernal-grass (*Anthoxanthum*), with unpleasing taste and said to be mainly responsible for hay-fever, flrs. appear very early and have only 2 sta., very typical of meadows; Oat (*Avena*), with long twisted awns, very susceptible to changes in the moisture of the air; Cock's-foot Grass (*Dactylis*), with all flrs. to one side, characteristic of meadows; Fescue (*Festuca*), important fodder-grasses; Barley (*Hordeum*), with very long rough awns; Rye-grass (*Lolium*), in meadows, infl. flat with spikelets in two rows; Cat's-tail Grass, Timothy-grass (*Phleum*); Reed (*Phragmites*), swamp-plant, sometimes 16 ft., lower flrs. in each spikelet ♂; Meadow-grass (*Poa*); Marram-grass (*Psamma*), on sand-dunes; Wheat- or Couch-grass (*Triticum*), with spikelets compressed at right angles to main axis.

The following genera are cultivated as cereals: Oats (*Avena*), Barley (*Hordeum*), Rice (*Oryza*), Rye (*Secale*), Millet (*Sorghum*), Wheat (*Triticum*), and Maize (*Zea*).

CHAPTER XXX

HEREDITY AND EVOLUTION

IT will be a matter of common knowledge that the offspring of either plants or animals resemble their parents very closely. This fact, though so obvious, really involves the fundamental principle of *inheritance, i.e.* the progeny inherit the characteristics of their parents. Thus, if we sow the seeds obtained from a self-pollinated flower of the Foxglove, the numerous resulting seedlings obviously inherit the same general characters. Closer observation, however, shows that there are many minute points of difference which may in the main be related to the fact that the conditions in the seed-bed are not uniform (cf. also Fig. 153). The features presented by any particular individual may, as a matter of fact, be regarded as the outcome or resultant of two sets of factors, being either inherited or due to the effect of the environment. Under *environment* we understand all the external influences—physical, chemical, and biological—to which the organism is subjected. In the case of plants, and still more in that of animals, the conditions of the environment are not constant throughout the life of the individual, but in general it is those experienced in the early stages of development which are most potent in moulding the organism.

Individual variations, though probably in the main correlated with differences in the environment, may well also result from changes in the internal conditions which are more difficult to analyse. Such variations may be of two kinds. They are *qualitative* or *substantive*, when, for instance, they concern the shape or size of the entire plant (Fig. 153) or of any of its parts, the degree of hairiness, the type of colouration (Fig. 154), etc. On the other hand, they are *quantitative* or *meristic*, when they involve differences in the number of constituent parts, such as perianth-segments, leaflets in a compound leaf, etc.

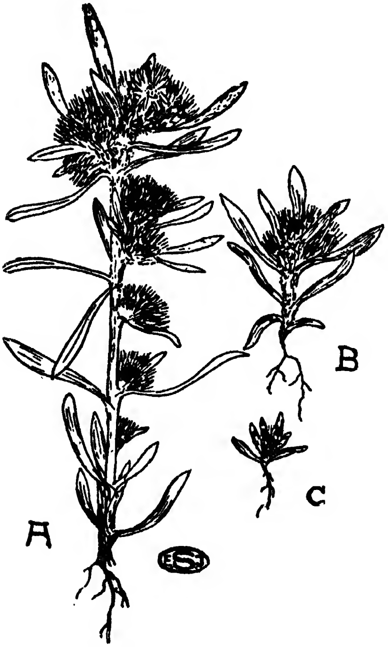

Fig. 153.—Three equal-aged individuals of the Marsh Cudweed (*Gnaphalium uliginosum*) from the same locality, showing individual variation. All three are in fruit. (Natural size.)

It is easiest to study variation if some character is selected which is capable of exact measurement, as, for instance, the length of the leaf in the Privet, the length of the Runner Bean seed, or the number of ray-florets in the Daisy. Taking the first of these cases as an example, it will be found that if, say, a thousand leaves are measured, the difference between the length of the shortest and the longest is quite considerable, and that the majority of the leaves are of an average size. If all the thousand leaves be classified according to their lengths into separate groups, differing by increments of one millimetre, and the number of leaves in each group counted, those containing the smallest number will be found to be situated at the two extremes. Between these points the number of leaves of each particular length will be found to increase with considerable regularity, as the size of its individuals approaches that exhibited by the majority. This most frequent size is termed the *mode*, and often corresponds very closely to the arithmetical mean of all the measurements.

By plotting a curve, in which the ordinates represent the number of individuals in each group, and the abscissæ the respective lengths, the variation can be graphically represented

(Fig. 155). The larger the number of individuals taken into account, the smoother the outline of the curve. Such *variation curves* are most commonly symmetrical (Fig. 155, left), but they may be one-sided or asymmetrical (Fig. 155, right), as in the case of the meristic variation of the corolla-segments of many flowers, where there are often relatively few examples with *less* than the normal number of parts.

The normal symmetrical curve of variation agrees very closely with that representing variation depending on pure chance, a feature which in itself suggests that the manifold differences in the conditions of the environment are involved. The classical example of such chance variation is afforded by the repeated tossing up of two coins, the combination of one head and one tail being most frequent (forming about 50 per cent. of the cases), whilst the combinations two heads or two tails occur with about equal infrequency. A more illustrative curve of chance variation would be obtained if ten coins were tossed simultaneously for a large number of times in succession.

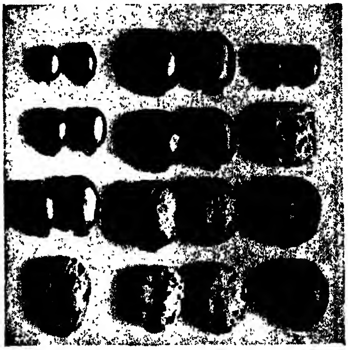

FIG. 154.—Seeds of different varieties of Castor Oil (*Ricinus*), to illustrate variation within a species. [Photo E. J. S.]

In cases of meristic variation it will be noticed that the difference between the extremes is much greater when the mode corresponds to a large number than when it coincides with a small one. Thus, if variation due to fission of parts (say of the corolla of a flower) be equal in two species, the one having a mode of five (*i.e.* usually five petals) and the other having a mode of ten (*i.e.* usually ten petals), there would be just double the chances of fission occurring in the latter as in the former. The extreme condition (*i.e.* 10 and 20 petals) would be attained where all the petals underwent fission. That is, the range would be greater in the one case than in the other, although the actual frequency of fission of the individual segments was the same in the two species. Hence a comparison of variation in two cases, where the modes are dissimilar, can only be made by taking such dissimilarity into consideration, a comparison of the curves alone being misleading. The position of the mode can often be to some extent changed by modifying the environmental conditions, although the range of variation remains practically unaltered.

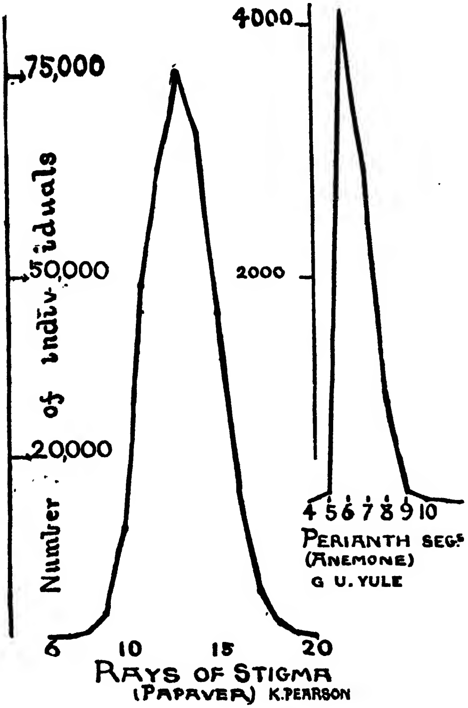

FIG. 155.—Variation curves, symmetrical on the left and asymmetrical on the right.

It appears that individual variations are not inherited, and that in a *pure line* of descent the average of the race is maintained.[1] This has been established by sowing seeds from a single individual of pure descent which has been self-fertilised, the seed produced by the resulting plants (likewise self-fertilised) being sown in separate groups, and the same procedure followed for several successive generations. It was thus found that the average size of individuals derived from small parents is practically identical with that of individuals grown from large parents; also that heavy seeds do not beget heavier-seeded offspring than those derived from light seeds. The following data, which serve

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[1] By a pure line is understood a pure-bred strain produced by self-fertilisation from a single individual.

to illustrate this point, are taken from Johansen's experiments with Beans which were self-pollinated:

Weight of seeds of parents.	Average weight of seeds of offspring.
350–400 mg.	572 mg.
450–500 „	535 „
500–550 „	570 „
550–600 „	565 „
600–650 „	566 „
650–700 „	555 „

When dealing with a population consisting of members possessing varied hereditary constitution (*i.e.* not a pure line), a pure strain can often be obtained by selecting individuals which show a particular desired character and breeding from these, with due precautions against cross-pollination. In this way it might, for example, be possible by *artificial selection* to obtain pure lines, exhibiting a tall or dwarf habit. Under natural conditions the environment may often exercise such a selective influence (so-called *natural selection*). The possession of a particular character is sometimes decisive in determining which plant shall survive in competition with others, against adverse conditions of climate, etc. Even in a pure strain, some selective action might lead to the elimination of all but the heaviest, shortest, etc., individuals in each successive generation. This was the essence of Darwin's theory of the origin of new species.

The majority of plants produce such an abundance of spores or seeds, as the case may be, that even with the most efficient dispersal it would usually be impossible for all the offspring to become established. Many a common plant would, indeed, if the means of dispersal were adequate, and all the progeny of successive generations survived, rapidly cover a large surface of the globe. That this does not happen is due to that ceaseless competition of living organisms with one another which is known as the *struggle for existence*. A Mullein plant, for example, may produce as many as 700,000 seeds. The resulting seedlings are not of equal vigour, and those first to succumb in the struggle for existence are obviously the weakest. The latter, applying the term in its widest sense, owe their lack of vigour partly to adverse environmental conditions and partly to inherited characteristics. Just as a human being with a "weak constitution" may have inherited his defect or owe it to the surroundings in which he grows up.

Unlike most animals, plants cannot choose their place of habitation. The seeds or spores are carried passively to a variety of situations, and their chances of developing into mature plants depend upon their power of accommodating themselves to the environment in which they may be placed. But many plants exhibit this power of *adaptation* to a very marked degree, as, for instance, certain aquatics (Water Starwort, *Callitriche*; Water Crowfoot, *Ranunculus aquatilis*; Water Milfoil, *Myriophyllum*) which can grow either totally submerged or on exposed mud. The ordinary aquatic form of such plants has much elongated stems bearing very delicate or finely divided leaves and slender unbranched roots, whilst large air-canals (Fig. 87) traverse all the different organs; moreover, the xylem is exceedingly reduced, since water can be absorbed over the whole surface. In the so-called land-forms, however, the internodes become extremely short, so that the whole plant is very stunted (cf. Fig. 156, L); further, the leaves are much thicker and smaller (Fig. 156, L) and, when divided, show broader and fewer segments, whilst the roots are more strongly developed. As regards the internal structure, such a land-form shows far smaller air-spaces, an increase of water-conducting tissue, and a thicker cuticle, whilst stomates are present in the leaves. Similarly, when a terrestrial species grows both in sunny and shady situations, the sun-form is adapted to its environment by reduction of the leaf-surface (cf. p. 164), sinking of the stomata (cf. p. 130), etc.

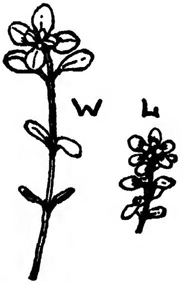

FIG. 156.—Land-form (L) and Water-form (W) of the Water Starwort (*Callitriche*). (Natural size.)

It has long been a matter of dispute as to whether or no such changes, impressed upon an organism by the environment, bring about any corresponding internal modification by means of which the new characters can be transmitted to the offspring. So far all attempts to demonstrate satisfactorily the inheritance of such *acquired characters* have proved a failure. It is indeed difficult to conceive of any plausible means by which characters, acquired by the plant in the course of its lifetime, could affect and modify the hereditary mechanism which must obviously be contained within the fusing gametes. On the other hand, the marked adaptations of plants in the wild state to their normal environment, features often retained when the organism is transferred to another habitat, naturally suggest the possibility of the unstable acquired characters becoming ultimately stabilised. This view has led to the conception of the origin of new species, etc., through cumulative selection and hereditary transmission of favourable variations (or mutations, cf. below), tending towards more complete harmony between the plant and its environment. Another point, upon which there is much difference of opinion, is the actual influence of the environment in moulding the structure of a plant. Whilst some consider that adaptation to the environment is due to selection, others believe in a direct response to changed surroundings.

Seeing that the individual variations above considered are all encompassed within the apparently fixed range of the species (cf. p. 320), they could scarcely seem to have led to the evolution of new forms. But in carefully selected and self-fertilised cultures of the higher plants, and even in pure cultures of lower organisms, it has been found that slight or pronounced departures from the mode occasionally arise which breed true to their new characters from the very first, *i.e.* these are hereditarily transmitted. Such *mutations*, which are sometimes far more pronounced than the individual variations, and consequently obvious even to superficial observation (Fig. 157), may well be responsible for the origin of new species. As to the causes of mutation we are, however, in complete ignorance, though it is tempting to assume that the external environment is the stimulus that brings about the internal change. If this could be experimentally proved, many of the divergent views at present held could be harmonised.

A familiar instance of a mutation is afforded by the Irish Yew (*Taxus baccata*, var. *fastigiata*), which differs from the common Yew, from whence it arose, in its darker foliage and Cypress-like habit. Detailed studies of mutations were first made by De Vries on a species of Evening Primrose (*Œnothera lamarckiana*), which occurred as an escape in a field near Amsterdam, where it was found producing a considerable number of

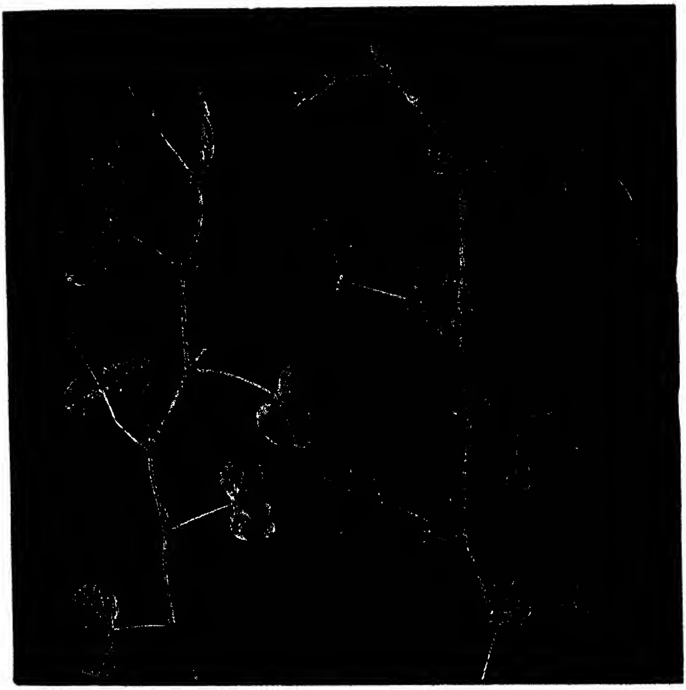

Fig. 157.—A new form or mutant which arose from a pure strain of Duke of Albany Pea and which differs in the narrow lanceolate stipules. The type on the right, the mutant on the left. [By permission of Prof. Bateson, F.R.S., and Miss Pellehew.]

new forms, which subsequently bred true. For instance, one form was distinguished by the possession of broad leaves, another by red-veined leaves, others by dwarf- or giant-habit, and so on, as the following epitome of some of De Vries' cultures shows.

MUTATION IN *ŒNOTHERA LAMARCKIANA*

(The horizontal lines show successive generations, invariably obtained only by sowing seeds of the ordinary form.)

	Giant Form.	White-leaved Form.	Oblong-leaved Form.	Red-veined Form.	Normal Form.	Dwarf Form.	Broad-leaved Form.
I	—	—	—	—	9	—	—
II	—	—	—	—	15,000	5	5
III	—	—	—	1	10,000	3	3
IV	1	15	176	8	14,000	60	73
V	—	25	135	20	8,000	49	142
VI	—	11	29	3	1,800	9	5
VII	—	—	9	—	3,000	11	—

Since it has been suggested that De Vries' mutants sprang from an originally hybrid stock (cf. below), it may be mentioned that other instances of mutation have since been described in which the pure-bred character of the original strain appears to be beyond question. Moreover, mutations do not occur only in plants raised from seed, where as a consequence two gametes are involved. The propagation of *vegetative mutations*, or *sports*, which first appear only on a few branches of the plant, has given rise to the cut-leaved varieties of Alder, Beech (Fig. 158), etc., the leaves of which are normally undivided.

Another mode of origin of new forms is due to the recombination of characters which takes place when two different races, varieties, or species are employed as the respective parents. In such cases the fertilised eggs are, of course, produced by the participation of both parents, one furnishing the female and the other the male sexual cell. Such " crossing " is often a failure, no seed being set, but when successful the next generation is found to show a mixture of the characters of the two parents, some belonging to the one and some to the other.

In respect to any single contrasting feature (*e.g.* height, hairiness, etc.), however, the character of one or other parent frequently altogether predominates (*i.e.* the offspring all show the one feature), although sometimes the *hybrid* is intermediate between the two (cf. p. 330). Since the characteristics of both parents must have been inherited, those of the one must, in the former case, be supposed to remain dormant, or, as is usually said, *latent*. As a matter of fact, if such hybrid plants are self-fertilised, the latent character reappears in a certain number of the individuals arising from the resulting seeds, a fact which proves that it must have been present, although not outwardly manifest.

An exact study of the phenomena of *hybridisation* was first undertaken by Mendel, an Austrian monk, by considering the behaviour of single pairs of characters only. In one of his earliest experiments he crossed tall and dwarf Peas, the whole of the resulting offspring (first generation) being tall. The seeds produced from these, by self-fertilisation, afforded two classes of individuals, three-quarters being tall and one-quarter dwarf. But of these tall Peas of the second generation (if again self-fertilised) only one-third bred true, the remainder behaving just like the original hybrids of the first generation, and giving rise to talls and dwarfs in the proportion of three to one. The dwarfs in every case bred true. In the second generation of such a cross, then, as regards any one particular pair of characters, half the offspring are pure (one quarter resembling one parent, another quarter the other parent), whilst the other half are impure and bear the characters of both. Representing the tall Pea by *T* and the dwarf Pea by *d*, these results can be graphically expressed as follows:

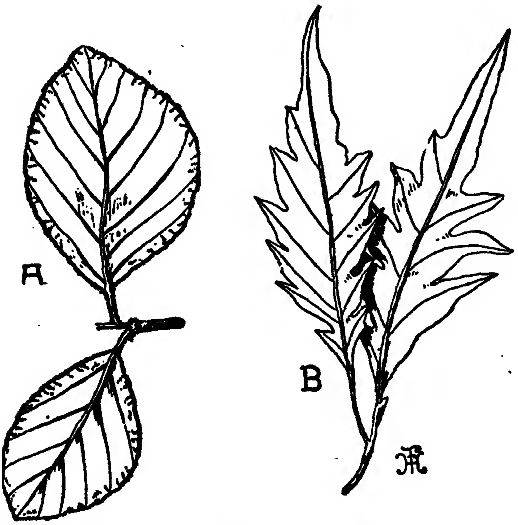

Fig. 158.—Twigs of A, ordinary Beech, and B, cut-leaved Beech, illustrating a vegetative mutation.

First generation: Td (all tall).

Second generation: $1T$: $1d$: $2Td$ (one tall, one dwarf, two hybrids).

A considerable number of other pairs of characters have been studied in the same way, with identical results, though there are a number of exceptions, some of which are at present inexplicable.

The latent character is usually spoken of as the *recessive* and the other as the *dominant*. In the experiment with tall and dwarf Peas above described, where the difference is one of size, there is reason to believe that the dwarf habit is due rather to the absence of a character causing tallness than to the presence of a special character for dwarfness. And it may well be that in all cases the recessive character is caused by the absence of something which determines the dominant (*e.g.* a non-hairy form of a particular plant may be due to the absence of a character for hairiness, etc.). Pairs of characters, which thus combine in the first hybrid generation and segregate in the subsequent generations, are termed *allelomorphs*. The following are further examples, the dominant character in each case being that first named.

Yellow and green, round and wrinkled seeds in Peas.
Prickly and smooth fruits (Thornapple, Field Buttercup).
Susceptibility and resistance to Rust in Wheat.
Starchy and sugary endosperm in Maize.
Hard (glutenous) and soft (starchy) endosperm in Wheat.

A feature which may be of great significance is that almost all the mutants so far studied behave as recessives to the parent stocks from which they sprang. It may be added that recent research has shown that many apparently simple characters can be analysed into a number of subordinate ones, which, however, are very commonly inherited together.

The most important principle, demonstrated by the experiments of Mendel and subsequent workers in this field, is that the characters introduced by either parent do not become inextricably intermingled in the hybrid offspring, but become separated out again in the gametes; that is to say, each of the latter bears only one allelomorph. It is only on this basis that the reappearance of a latent character in the second generation can be explained. If the dominant and recessive characters of an allelomorphic pair are represented by *A* and *a* respectively, then the fertilised eggs produced by crossing will all have the constitution *Aa*, and the resulting plants will all show the dominant character only; such individuals are spoken of as *heterozygotes*. There is reason to believe that in these hybrids, during the formation of each group of four spores, and in conjunction with the reduction division (see p. 274), the characters *A*, *a* become separated, so that each spore, and consequently each of the gametes, to which it ultimately gives rise, bear either *A* or *a*. It is probable, moreover, that the determinants for these characters are contained within the nuclei of the sexual cells (p. 333)

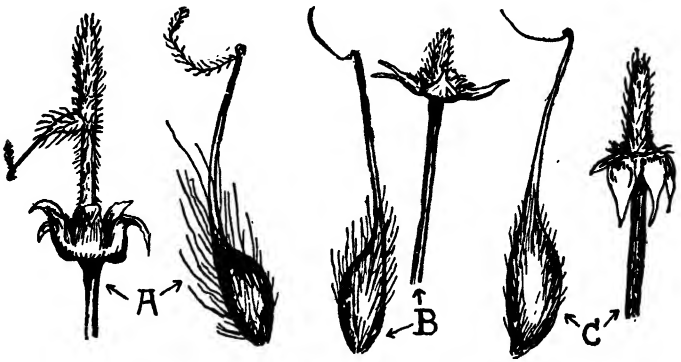

FIG. 159.—*Geum rivale* (A), *Geum urbanum* (C), and the hybrid between them, *Geum intermedium* (B). In each case the receptacle and calyx are shown, together with an enlargement of a single carpel.

During self-fertilisation, and assuming the gametes to meet according to the laws of chance, there are four possible combinations: viz. (1) a male gamete bearing *A* and a female bearing *A*; (2) a male bearing *A* and a female bearing *a*; (3) a male bearing *a* and a female bearing *A*; and (4) a male bearing *a* and a female bearing *a*. That is to say, among each four fertilised eggs that result, there will probably be 1 *AA*, 2 *Aa*, and 1 *aa*. Seeing that *A* is invariably dominant, there will in the second generation be three individuals with the dominant to one individual showing the recessive character; of the former, however, two will be heterozygotes, which would exhibit segregation according to the same principle in the ensuing generation, whilst the other, as well as the individuals possessing the recessive character, are *homozygotes.*

Further evidence, in support of this hypothesis, is furnished by the result of crossing the hybrid of the first generation with one or other parent (*i.e.* $Aa \times AA$ or $Aa \times aa$). In this case only two kinds of combinations will be obtained, viz. taking the case in which the hybrid is crossed with the parent-form having the dominant character, AA and Aa, and there are obviously equal chances for either combination to occur. The second generation of such a cross does, as a matter of fact, afford individuals half of which are hybrid and half pure. Moreover, when it is recalled that the endosperm of Angiosperms develops as the result of a nuclear fusion (p. 294), it is of interest to note that, if varieties of Maize possessing different types of endosperm (*i.e.* variously coloured or containing sugar and starch respectively) are crossed, that of the resulting seeds exhibits evidence of its hybrid origin.

If two pairs of characters are considered, it has been found experimentally that, whilst the first generation consists only of hybrids showing both dominants, the second comprises a number of distinct individuals occurring in the following proportions: 9 with both dominant characters, 3 with one dominant and one recessive, 3 with the other dominant and the other recessive, and 1 showing both recessives. The relations will be plain if the diagram in Fig. 160 is studied. Thus, if yellow round Peas are crossed with green angular ones, the first generation all bear yellow round Peas; in the second generation there will be 9 yellow round, 3 yellow angular, 3 green round, 1 green angular. Of the nine individuals showing both dominant characters one only breeds true, as also does the one bearing both recessive characters. The remainder, on being self-fertilised, exhibit segregation according to the particular characters which they contain.

The dominance of a character is only important for the elucidation of the observed facts in the many cases where dominance occurs. But the principle of segregation is equally applicable where the heterozygote is intermediate between the two parents, or, as in some cases, even differs from both. A hybrid intermediate between the two parents is obtained, for instance, when the Star and Chinese Primroses are crossed. The petals in the first generation are intermediate in character between those of the two parents (Fig. 161); in the second generation segregation takes place in the usual way, the hybrid-individuals (one-half) still exhibiting flowers of the

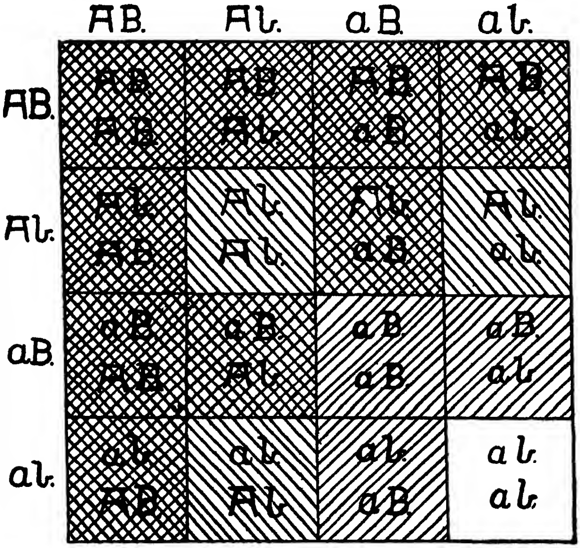

FIG. 160.—Scheme to illustrate the progeny of the second generation when two pairs of characters (*Aa*, *Bb*) are taken into consideration. The individuals of the first generation will all have the constitution *AaBb*. When segregation occurs, the resulting gametes will have the four possible constitutions *AB*, *Ab*, *aB*, *ab*,[1] and the scheme shows the possible methods of combination of such gametes. When both dominants are present (in nine out of the sixteen cases) the squares are cross-hatched, when the dominant *A* is present the shading slopes from left to right, when *B* is present from right to left; when neither dominant occurs the square is left unshaded.

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[1] The combinations *Aa* and *Bb* do not arise, since dominant and recessive characters are segregated.

intermediate type, whilst the remainder consist of Star and Chinese Primroses in equal numbers.

Hybridisation experiments not only teach us the principle of segregation of characters, but also emphasise the fact that external appearance is no certain guide to the internal characteristics. This is perhaps most strikingly illustrated by the effect of crossing certain pure-bred strains of white-flowered Sweet Peas. We should naturally expect all the offspring to be white-flowered too, but in reality all have coloured flowers, with a purple standard and blue wings. Here, clearly, the parents possess characters which *in combination* lead to the production of a coloured flower, though when separated they produce no visible effect. By breeding plants the limited knowledge of the constitution of any organism, which is obtained by mere examination of external or internal structure, can thus be to some extent supplemented.

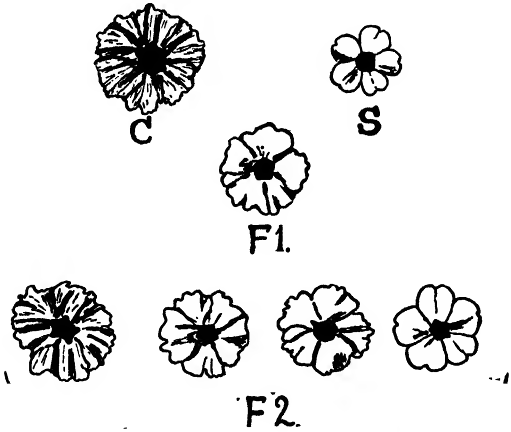

FIG. 161.—Hybrids between Chinese (*Primula sinensis*) and Star Primroses (*P. stellata*). At the top the two parents, the Chinese (*C*) with large, rather wavy, much crenated petals, and the Star (*S*) with smaller flat petals exhibiting only a notch. The F1 generation is intermediate between the two in these respects. In the F2 segregation takes place in the usual way. (After Punnett.)

When two varieties cross in nature, the appearance of the hybrid is of course influenced by all the characters present in the parents. Whether it resembles one or other parent, or is roughly intermediate between them, will depend on whether one parent contributes a greater proportion of dominant, or more conspicuous, characters than the other. Common examples of such hybrids in the wild state are afforded by various Willows, *Geum intermedium* (Fig. 159, B), *Quercus intermedia*, etc.

It has long been familiar to gardeners that shoots, which show a mingling of the characters of scion and stock, are sometimes produced as a result of grafting (cf. p. 205). The intermediate nature of these so-called *graft-hybrids* appears to be due to the fact that both scion and stock contribute to their development, the tissues of the one forming a skin over those of the other. The character of the seeds, and of the resulting offspring, is determined by the member responsible for the formation of the subepidermal layer from which the sexual cells are ultimately derived. This explains the fact that the seeds of graft-hybrids always breed true to the characters of either scion or stock. The commonest example of such a graft-hybrid is that known as *Cytisus adami*, which is due to the grafting of the Purple Broom (*Cytisus purpureus*) on the Laburnum (*C. laburnum*).

It has been repeatedly noted that the fusion of the nuclei of the gametes appears to be the most important step in *sexual reproduction*. This is supported by the fact that, in all the higher plants, the male cell consists of little else than the nucleus (cf. pp. 259, 294), and that, in hybrid-experiments, it is immaterial whether the one or the other parent is employed as the male.[1] The nucleus has also been seen to play a very important part in the activity of the cell, and, when dividing, to pass through a very complex series of changes. These have as their outcome an equal distribution of the chromatic material, which indeed is the only part of the nucleus that remains recognisable throughout all the phases of division. It may therefore be reasonably supposed that, in some way or other, the chromatin is the carrier of the hereditary qualities of the organism.

Sexual fusion may then be regarded as operating in two ways, firstly as a stimulus leading to further development,

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[1] Some forms of *Œnothera* and *Epilobium* appear to constitute an exception to this generalisation.

secondly as a possible means of introducing new characters or of rearranging those already present in the two parents. The former result may be attained by other stimuli. Amongst animals, for instance, the eggs of the Frog have been caused to develop by mere pricking with a glass needle covered with blood-serum, and those of Sea-urchins by treatment with solutions having a higher osmotic pressure than sea-water. Amongst plants the Orange, with several embryos in its seeds, furnishes an analogous example; here certain cells, apart from the fertilised egg, have developed into embryos, but there is no evidence that the apogamously produced seedlings are any less vigorous than those resulting from sexual fusion. It seems probable, therefore, that the chief advantage of sexual reproduction lies in the possibility of producing organisms, with a slightly different hereditary constitution, such as may survive under conditions that would be unfavourable to the pure parent strain. In other words, sexual reproduction provides material upon which natural selection can operate.

The *segregation of characters* above referred to is most probably effected during the reduction division in the spore mother-cells. In this process the chromosomes, instead of splitting longitudinally, as in the vegetative divisions, separate in their entirety into two sets. These pass to the respective daughter-nuclei, so that, of the four resulting spores, two possess the characters borne by one set, and two those borne by the other set. If this hypothesis be true, the separating members of a pair of chromosomes probably originate from the respective parents. In an allelomorphic pair one character (*e.g.* the dominant) is assumed to be present in one chromosome of a pair and the recessive in the other. In the reduction division, therefore, the allelomorphs will become separated, so that pure recessives and pure dominants can be bred. Such a theoretical conception is incapable of proof, and it is only warranted because it tallies with the observed facts.

In *vegetative propagation* the offspring normally exhibit no change of character, as compared with the parent, and new forms can only arise by mutation. Mutations in vegetatively produced offspring, and even in certain branches of an individual, have indeed been occasionally observed (cf. p. 325), and may be the means of maintaining the race in harmony with its environment. Although vegetative mutation appears to be comparatively infrequent, it should be borne in mind that some groups (*e.g.* Bacteria), which multiply exclusively by vegetative means, often do so with great rapidity. An exceptionally large number of generations is therefore formed in a short time, and so presumably the opportunities for mutation are proportionately great.

The *theory of evolution* explains the resemblances between the members of a genus or family as the necessary consequence of their origin from a common ancestor or from closely related forms. It has already been seen how new types can arise as a result of mutation or hybridisation. Since these show a great resemblance to their known parents, it is reasonable to regard the many features in common, between species of a genus or between the genera of a family, as indications of a natural affinity between them.

The different species, genera, and families of plants are very unequally spread over the surface of the earth, some (*e.g.* Chickweed) having an almost world-wide distribution, whilst others are restricted to certain parts; moreover, the same species may often be found in two or more widely separated regions, though altogether wanting in the intervening area (cf. below).

Geological research has shown that oceans and continents have undergone manifold changes, even during the period of existence of many living species, and these secular changes probably afford the clue to the discontinuous distribution of many species and families.

The natural barriers to the spread of plants are oceans, mountain ranges, deserts, etc., and it is significant that isolated islands (*e.g.* New Zealand) are peculiarly the home of species, so-called *endemics*, which are found there and there alone. There is, moreover, good reason for believing that, in a region devoid of natural barriers, the area over which a species is distributed is proportional to the age of the species or the time that has elapsed since its introduction. The capacity of a species to extend its range in new territory depends on an efficient seed-dispersal, the rapidity of its spread by this or by vegetative means, and its vigour in competition with others.

Certain groups, now represented only in widely separated areas over the earth's surface (*e.g.* the Cycads, a group of Gymnosperms found only outside Europe), are known from the fossil records to be ancient, and may well have attained their wide distribution before the present barriers were as pronounced or had even become established. A similar instance is furnished by the occurrence of the same Arctic species on the tops of many high mountains, although the present-day climate of the plains offers an insurmountable barrier to their dispersal from one chain to the other. These plants may, however, well represent the last remnants of a widespread flora of glacial times which, when the ice-sheet melted, found suitable conditions only on the mountain summits.

The conception of evolution regards the organic world, as we find it to-day, as consisting not of a number of immutable forms, but as presenting one phase in an everchanging series. The organisms of the present are the offspring of those of the past, and will themselves, in turn, give rise to the organisms of the future. The large numbers of animals and plants which have become extinct must be supposed to have failed to "make good" in the competitive struggle. From the fossil records it is known that whole floras and faunas have thus perished, leaving no living representatives or only much modified descendants. Such disappearance may well be an outcome of the secular, but none the less profound, changes that have marked the history of the earth's surface since life first appeared. Organisms, unsuited to the new conditions, would inevitably perish as a result of being handicapped in competition against, either their more adaptable contemporaries, or new forms which were better equipped to withstand the changed environment.

The evolutionist conceives of all life as having developed from relatively simple undifferentiated unicellular organisms, many of whose descendants, through the ages, have gradually acquired an increasing complexity of structure in relation to progressive division of labour. On this hypothesis, if our knowledge of all the extinct plants of former eras were complete, we could reconstruct the genealogical history (*phylogeny*) of the present-day forms. Those of the past would furnish the links connecting genus with genus, and family with family, till all were connected up to the primitive simple organisms from which they sprang when life first developed. The fact that many fossil plants and animals do combine characters, that now serve to distinguish separate groups, is one of the strongest pieces of evidence for such a conception. But, further, the geographical distribution of living plants and animals, showing as it does restriction of similar species to definite areas, is most readily

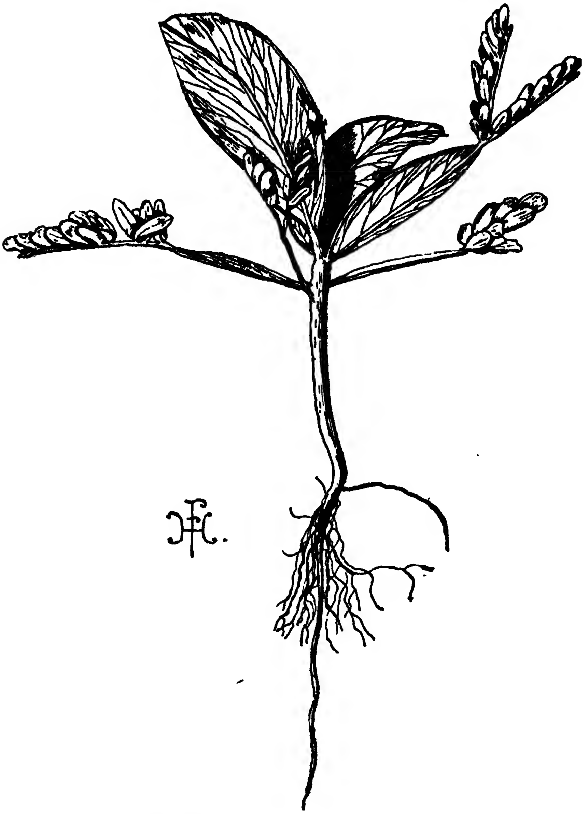

Fig. 162.—Seedling of an *Acacia*, showing the gradual flattening of the petioles, and suppression of the laminæ, in leaves of successive ages.

explained as due to their origin, in that area, from common or closely related parents.

The features characteristic of the various members of a genus or family are often only fully apparent in the adult state, whilst the earlier the stage of development of an organism, the more difficult does the determination of its identity become. The history of the individual may be regarded as, to a limited extent, recapitulating the history of the race; in this connection it may be noted that in the ordinary course of reproduction every individual commences life as a single cell. Such an interpretation also explains the frequent occurrence of rudimentary structures (*e.g.* the gill-slits in the embryo of the Chick, or the pinnate leaves in the seedling stages of species of *Acacia* (Fig. 162), later possessing highly modified leaves), which often perform no function, or are even completely lost, in the adult. Even amongst living organisms a graduated series, as has been seen in Chapters XXII to XXVIII, can be recognised. The simplest members of this series are doubtless relics, though almost certainly modified, of the earliest flora and fauna, which have found a place in the economy of nature even under existing conditions.

The highest efficiency is only attained by great specialisation which proportionately diminishes the capacity for adaptation to a new environment. But the world of living things is a world of never-ceasing change, and hence the past history of the organic universe is the history of extinction of specialised races and individuals. The future of a group is thus seen to be dependent upon its less specialised, and thus at the moment less successful, members. But as in time, so too in space, the spread of a species may be handicapped by its lack of plasticity.

Some of the groups we have been unable to consider, for instance, the extinct Club-mosses and Horsetails, in the era of their success, were more specialised and more complex than their present descendants, which play so subordinate a rôle, and probably owe their survival to features which characterised the less successful members of these groups in the past. Such considerations lead one to suspect that the subordinate groups and individuals of any one age are the most likely starting-points for the dominant vegetation of the next, and so we can understand why the fossil record presents us with abundant examples of clearly defined groups (*i.e.* of the prevalent successful forms) and comparatively few representatives of groups "in the making." Indeed, the fossil plants of past ages and the living organisms of to-day combine to emphasise the rarity of the "missing link" which, like the thinker in advance of his age, is not sufficiently in harmony with the environment to command success, but yet marks the beginnings of the facies of the future. It is not, therefore, surprising that our progress in the reconstruction of the genealogical tree of the Vegetable Kingdom is slow, and that many of the groups remain in striking isolation from one another.

APPENDIX

I. *Reagents.*—Details as to the mode of preparation of the principal reagents mentioned in this book are given in the following:

Ammoniated Copper Oxide (*Cuprammonia*).—This reagent must be freshly prepared. Add ammonium chloride, and subsequently excess of sodium hydrate, to a solution of copper sulphate. The blue precipitate produced is filtered and washed thoroughly, and then dissolved in a small quantity of strong ammonia.

Chlor-zinc iodide.—This is not easily prepared and, therefore, best purchased from some chemical firm. It only remains effective for a few weeks and must be used fresh.

Eau de Javelle (mainly potassium hypochlorite).—Mix 20 parts of chloride of lime with 100 parts of water. Allow to stand, and then add a solution of 15 parts of caustic potash in 100 parts of water. Filter after some hours and use the filtrate.

Fehling's Solution (an alkaline solution of cupric oxide).—According to Haas, this is best obtained by mixing equal quantities of a solution containing 69·28 grams of pure crystallised copper sulphate in 1 litre, and of a solution containing 350 grams of Rochelle salt (potassic sodic tartrate) and 100 grams of sodium hydrate in 1 litre. The resulting solution is of a clear dark blue colour. Ten cubic centimetres of this solution are reduced by 0·05 gram of glucose.

Iodine Solution.—This is made by dissolving crystals of iodine in a strong solution of potassium iodide. For use this is diluted to a light brown colour.

Millon's Reagent.—This is a mixture of mercuric nitrate and nitrite. It can be prepared by dissolving 15 grams of mercury in 30 grams of cold nitric acid (sp. gr. 1·42), which operation should be performed in a fume cupboard. Dilute with twice the volume of distilled water, and filter after two hours. This reagent can also be bought ready made from the usual dealers in chemicals.

Phenylhydrazine Hydrochloride (after Mangham).—Prepare separate solutions, in ten times their weight of glycerine, of phenylhydrazine hydrochloride and sodium acetate respectively. Place the material to be investigated in equal drops of these two solutions, thoroughly mixed, and, after covering with a cover-glass, heat for from one to several hours in an oven.

Phloroglucin.—Prepare a saturated solution in alcohol. Treat material with this for a short time, and then mount in strong hydrochloric acid.

Scharlach Red.—Prepare a saturated solution in a mixture of 70 parts absolute alcohol and 30 parts water by volume. Filter and keep well stoppered.

Sulphuric Acid.—For cellulose tests it is usual to employ the concentrated acid. *Great care must be exercised in its use,* and strong ammonia should be at hand to neutralise any drops that may be spilled.

II. *Method of marking radicles or plumules with Indian ink.*—The marking may be most conveniently carried out by using a piece of cotton stretched out on a short piece of bent fish-bone like an archer's bow. The radicle or plumule is laid along the edge of a ruler, and the marks are made by the stretched cotton, which is moistened with Indian ink.

III. *Artificial Sea-water.*—For this purpose Tidman's sea-salt, dissolved in distilled water in appropriate concentrations, can be employed; or a solution can be made according to the following formula given by Osterhout:

1,000	parts	sodium chloride (gram-molecular solution).
78	,,	magnesium chloride (gram-molecular solution).
38	,,	magnesium sulphate (gram-molecular solution).
22	,,	potassium chloride (gram-molecular solution).
10	,,	calcium chloride (gram-molecular solution).

This solution has an osmotic pressure of about 22·4 atmospheres; when diluted with an equal volume of distilled water, the osmotic pressure is halved, when diluted with twice its bulk of distilled water the osmotic pressure is one-third of that of the undiluted solution, and so on.

IV. *The Compound Microscope* (Fig. 163).—This consists, essentially of a stand which has for its purpose the appropriate support and adjustment of the optical parts. The latter comprise two systems of lenses, known respectively as *ocular* (*Oc.*) and *objective* (*Ob.*), whilst accessory structures are constituted by a mirror (*M.*) for reflecting light, and, in better instruments, a *condenser* (*Co.*) for concentrating light upon the object.

The stand consists of a heavy *foot* or base (*Fo.*), bearing a rigid upright *pillar* (*L.*). To the latter the remaining portions of the microscope are hinged in such a way that the whole can be employed either in a vertical or in an inclined position. The part actually hinged to the pillar is known as the *limb*, and to this the flat *stage* (*S.*) is attached, at right angles, at the lower end, and the *body tube* (*T.*) towards the upper end. The stage, which is usually square, is perforated by a central aperture through which the light from the mirror reaches the object. In transferring the microscope from place to place, it should always be carried by the non-movable parts.

The body tube is a hollow cylinder, usually of brass, and is adapted to take the *ocular* or *eyepiece* (*Oc.*) at its upper, and the *objectives* (*Ob.*) at its lower, end. In order to secure rapid change of magnification, a *nosepiece* (*N.*), bearing two or three objectives, is screwed into the lower end of the body tube; by simply turning this a different objective can be brought to bear on the object. The distance between eyepiece and objective can be increased or decreased by pulling out or pushing in the draw-tube (*D.t.*), which is fitted into the upper end of the body tube. In order to focus the object clearly, the entire system of lenses can be moved nearer to, or farther from, the stage by means either of the coarse or fine adjustments. The *coarse adjustment* usually consists of two large milled heads (*C.*) on either side of the limb, and by turning either of these, which actuate a rack and pinion mechanism, a relatively large movement is brought about. The *fine adjustment* is generally operated by a single milled head (*F.*), situated at the top of the limb, and by this means a very slight movement is effected, enabling great accuracy of focussing to be attained.

Below the stage is fixed an adjustable aperture, the *diaphragm* (*D.*), by means of which the amount of light reaching the object on the stage can be regulated. If a condenser is present, it is placed between the diaphragm and the stage, and, in the best instruments, its distance below the stage is adjustable by means of another milled head (*H.*). The mirror (*M.*), which is concave on one surface and flat on the other, is either attached to the underside of the stage or (as in the type illustrated) forms part of the adjustable system bearing the condenser.

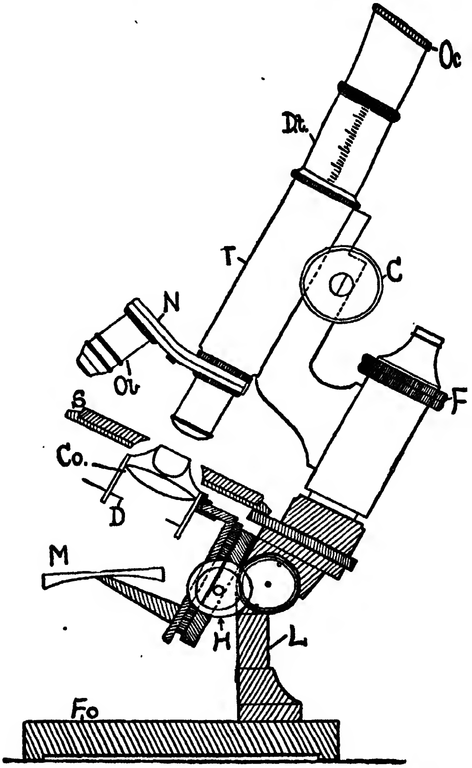

Fig. 163.—Diagrammatic representation of a compound microscope. *C.*, Coarse adjustment; *Co.*, condenser; *D.*, diaphragm; *D.t.*, draw-tube; *F.*, fine adjustment; *Fo.*, foot; *H.*, milled head controlling substage adjustment for condenser; *L.*, pillar; *M.*, mirror; *N.*, nose-piece; *Ob.*, objective; *Oc.*, ocular or eyepiece; *S.*, stage; *T.*, body tube.

The objectives most commonly in use are $\frac{2}{3}$ in. and $\frac{1}{6}$ in.,[1] which designations imply that, when focussed upon the object, they are approximately two-thirds and one-sixth inch respectively from the latter. These distances are the focal lengths, and the smaller they are the greater is the magnifying capacity of the lens. As a consequence, the longer focus lens is often spoken of as the *low power*, and the short focus lens as the *high power*. The image formed by the objective is projected on to the eyepiece, where it becomes further magnified. The amount of magnification of the eyepiece is commonly indicated by a number engraved upon it.

The object to be examined, mounted on a glass-slip in water or some other appropriate fluid and covered with a cover-glass, is placed on the stage, and light is projected on to it from below by means of the mirror. If a condenser is present, the flat side of the mirror is employed, but if not the concave side. To focus the object, *gradually* lower the tube by means of the coarse adjustment till the image becomes clear, and then turn the milled head to and fro until the image appears most distinct. Proceed in the same way when using the high power, but exercise the greatest care not to bring the objective in contact with the cover-glass, and *immediately* the image *begins* to appear use the fine adjustment only. The aperture of the diaphragm should be diminished till the maximum amount of detail is visible, whilst by adjusting the condenser the light reflected from the mirror can be accurately focussed upon the object.

In working with the microscope, it is best to accustom oneself to employ either eye. When drawing, view the object with the left, and sketch with the aid of the right, eye. As a first exercise in microscopic observation, it is well to examine the small air-bubbles almost invariably present in large numbers in a drop of water. Under the low power these appear as black dots or bright patches with broad dark margins; this dark border is due to refraction. Adjust the slide so that one of the smaller bubbles is in the centre of the field of view, and turn the nosepiece so as to view the bubble with the high-power lens. Using the fine adjustment, it will be noted that at a high focus the

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[1] **For the study of Bacteria and other minute organisms, higher powers are required, such as $\frac{1}{12}$ in. objectives.**

curved surface is seen and the outline appears shadowy, whilst at a lower focus only the circular equatorial portion (the *optical section*) is visible, and the outline becomes well defined.

V. *Preserving and Staining.*—To preserve material for anatomical investigation, ordinary methylated spirit will usually serve, provided there is at least four times the volume of liquid as of material. For showing nuclear structure, however, other fixatives are employed, *e.g.* acetic alcohol, made by adding one part of glacial acetic acid to four parts of alcohol. After remaining in this for a few minutes up to several hours, according to the texture of the material, the latter is transferred to ordinary spirit.

For staining, the thinnest sections (cf. VI below) should be placed in a few drops of safranin,[1] on a slide, for from five to fifteen minutes, more safranin being added at intervals to replace that lost by evaporation. The excess of the stain is now removed by washing the sections with spirit, and then a few drops of Kleinenberg's hæmatoxylin are allowed to act for half a minute. After this the sections are washed with spirit, and permanent preparations are made in the following way:

The spirit is changed several times, and finally replaced by a few drops of absolute alcohol. In this way dehydration (*i.e.* removal of water) is effected. To the alcohol a drop or two of clove oil is then added, and this mixture is in turn replaced by pure clove oil. The sections should now become transparent, and, if this fails to occur, they have not been sufficiently dehydrated. After two to three minutes the oil is poured off, and Canada balsam, dissolved in xylol, added. A cover-glass is then carefully let down on to the sections, and the slide placed on one side till the balsam sets. Throughout all these processes the greatest care should be taken that the sections are never without a covering of liquid.

If permanent preparations are not required, such stains as phloroglucin, aniline chloride, etc., can be employed to differentiate the tissues, and the sections are usually mounted in glycerine diluted with an equal volume of water. Preparations can also be mounted in glycerine jelly, such mounts being much

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[1] Or methyl blue can be used, the sections being left in this for about half a minute.

more rapidly and easily prepared than those with Canada balsam, but they often perish after a few years.

The liquid stains most commonly employed are prepared as follows:

Aniline Blue.—Saturated solution in alcohol or water, with a trace of acetic acid.

Bismarck Brown.—Dissolve 2 grams in 100 c.c. of 70% alcohol. Stain for about 1½ minutes.

Eosin.—1% solution in either water or alcohol. Stain for 3 to 5 minutes.

Gentian Violet.—1% solution in water. Stain for from 10 to 15 minutes, transfer to alcohol, and quickly counterstain with Bismarck brown.

Hæmatoxylin.—Best bought prepared ready for use.

Methyl Blue.—Saturated aqueous solution. For live staining this is greatly diluted.

Safranin.—1% solution in 50% alcohol.

VI. *Section-cutting.*—During this operation both razor and material should be kept moist with either water (for fresh material) or spirit (for preserved material). Hold the object between the thumb and first finger of the left hand, and arrange the tips of the remaining fingers so as to form a rest on which the razor blade can be glided backwards and forwards through the material. Note that the razor must be gently drawn through the object, and not pressed, as in ordinary cutting. The greatest care should be taken that the axis of the object is either at right-angles (for transverse sections) or parallel to the razor blade (for longitudinal sections). For the latter only a very short length of the stem, etc., should be used. When very thin objects, such as leaves, are to be cut transversely, small rectangular pieces, including a vein, are embedded in a vertical incision made in a short length of Elder-pith. Sections are then cut of the pith, as well as of the embedded object.

After cutting, transfer the sections to a slide, on which a drop of water or dilute glycerine has previously been placed, by means of a well-moistened brush, and reject all but the *two thinnest.* Complete sections are in most cases quite unessential, whilst the small fragments will usually be the thinnest. Oblique sections, even if thin, are quite valueless. The razor should be carefully cleaned by wiping it from the back towards the edge.

VII. *Method of passing a branch through a hole in a rubber cork* (after Osterhout).—A cork-borer, wide enough to take the branch, is passed through the hole in the cork, in the opposite direction to that in which it is desired to insert the branch. The latter is pushed some little way into the borer, which is then slowly withdrawn, thus leaving the branch in the cork.

VIII. *Auxanometers.*—The instrument described on p. 199 can be obtained from Messrs. Flatters & Garnett, 309 Oxford Road, Manchester, at a cost of about thirty-five shillings. A rather more expensive instrument, known as Farmer's Auxanometer, can be purchased for about £3 from any scientific instrument dealer. This instrument has a cylindrical drum which for use is covered with smoked paper and admits of readings being taken every quarter, half, or whole hour. Readings at such short intervals are, however, quite unnecessary for elementary experiments.

IX. *Preparation of pyrogallate of potash.*—This is obtained by dissolving 1 gm. pyrogallic acid in 15 c.c. of water and adding an excess of caustic potash (which should not be done until immediately before the experiment is started). This solution absorbs oxygen very energetically, as a result of which it takes on a brown colour.

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(Principal references are inserted in heavy type)