A TEXT-BOOK OF BOTANY

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INTRODUCTION

It is customary to place all living beings in either the animal or vegetable kingdoms, but in reality a sharp boundary line between animals and plants first becomes possible when they exhibit a complicated structure; while in those of more simple organisation all distinctions disappear, and it becomes difficult to define the exact limits of Botany and Zoology. This, in fact, could scarcely be otherwise, as all the processes of life, in both the animal and vegetable kingdoms, are dependent on the same substance, protoplasm. With more complicated organisation, the specific differences increase, and the characteristics distinguishing animal from vegetable life become more obvious. For the present, it must be confessed, the recognition of an organism, as an animal or a plant, is dependent upon its supposed correspondence with an abstract idea of what a plant or animal should be, based on certain points of agreement between the members of each class. A satisfactory basis for the separation of all living organisms into the categories of animals or plants can only be obtained when it is shown that all organisms distinguished as animals are in reality genetically connected, and that a similar connection exists between all plants. The method by which such evidence may be arrived at has been indicated in the THEORY OF EVOLUTION.

From the palæontological study of the fossil remains and impressions of animals and plants, it has been established that in former epochs forms of life differing from those of the present age existed on the earth. It is also generally assumed that all living animals and plants have been derived by gradual modification from previously existing forms. This leads to the further conclusion that those organisms possessing almost exactly similar structure, which are united as species in a genus, are in reality related to one another. It is also probable that the union of corresponding genera into one family and of families into a higher group serves to give expression to a real relationship existing between them.

The presumable origin of a living organism from others previously existing has been distinguished by HAECKEL (1) as its phylogenetic development or PHYLOGENY. He termed the series of changes passed through by a living being in attaining its mature condition its ontogenetic development or ONTOGENY. The supposition, that the successive steps in the ontogenetic development of an organism correspond to those of its phylogenetic development, and that the ontogeny of an organism is accordingly a more or less complete repetition of its phylogeny, was advanced by FRITZ MÜLLER (2), who based his conclusions on the results of comparative research.

The idea of the gradual evolution of higher organisms from lower was familiar to the Greek philosophers, but a scientific basis was first given to this hypothesis in the last century. Through the work of CHARLES DARWIN (3) in particular, the belief in the immutability of species has been overturned.

DARWIN is the author of the THEORY OF NATURAL SELECTION. In drawing his conclusions, he proceeds from the variability of living organisms, as shown by the fact that the offspring neither exactly resemble their parents nor each other. Further, he called attention to the constant over-production of embryonic germs, the majority of which must inevitably be destroyed. If this were not so, and all the embryos produced by a single pair attained their full development, they would alone, in a few generations, completely cover the whole surface of the earth. On account of insufficient space for all, the different claimants are engaged in an uninterrupted struggle, in which the victory is gained by those that, for any reason, have an advantage. Through this "struggle for existence," as only those organisms possessing some advantage live and mature, a process of enforced selection between the more fortunate survivors must result. In this manner DARWIN arrived at the supposition of a process of NATURAL SELECTION, which is the essential of his theory. Newly-developed peculiarities arising from individual variability must be inherited in order to become permanent characteristics of a later generation. That such characters are inherited is supported by the experience of breeders. The breeder selects individuals presenting any desired characters for the purpose of breeding, and has thus formed the races of domesticated animals and cultivated plants. These have often departed so widely from their wild ancestral forms that the latter are not certainly known. Just as in artificial selection, natural selection, although unconsciously, accomplishes this result. As individual peculiarities may be developed by careful breeding and rendered permanent, so by natural selection those qualities which are advantageous in the struggle for existence become more pronounced and are finally confirmed by heredity. By the continued operation of natural selection, organisms must result, which are, in the highest degree, fitted and adapted to their environment. Thus, by the survival of the fittest, through natural selection, that adaptability to the environment is gradually evolved, which is such a striking characteristic of organic life. That the transitional forms in this process of phylogenetic development no longer exist, is accounted for in the theory of natural selection by the assumption that the struggle for existence must necessarily have been most severe between similar organisms. For similar organisms have similar necessities, and the new and better-equipped forms must ultimately prevail over the original less specialised organisms, which, thus deprived of the essential requisites for their existence, finally disappear.

Since the publication of Darwin's works many investigators have laboured to advance and make clear our views on phylogeny. Botanists now endeavour to obtain an insight into the laws of phylogenetic development by systematic cultivation of particular plants. It would appear from such cultures (4) that the starting-point for the origin of new species is not afforded by the "fluctuating variations," which continually occur, but by more marked variations which have been termed "mutations"; these mutations appear suddenly and are strongly inherited. The tendency is to assume the existence of a development of the organic world due to original innate capabilities of the living substance and not dependent on selection. The origin of the large subdivisions of the animal and vegetable kingdoms, the "archetypes," would be due to this sort of evolution (5). These archetypes have been, and are still, continually influenced by the environment, and by their reaction to external conditions organisms have become more or less directly adapted. In this way striking resemblances in external form have arisen between organisms living under similar conditions although belonging to different archetypes (6). The progressive evolution of the archetypes as well as the direct adaptations to external conditions shown by them are independent of selection. The latter does, however, exert an influence on the process of evolution of the organic world, though to a much more limited extent than was formerly supposed. It acts especially when selection arises from the mutual relations of organisms; on the other hand it tends to render species distinct by removing the less advantageous variations which have arisen by mutation.

If the higher organisms have been evolved from the lower, a sharp distinction between plants and animals is excluded. For the characters which are distinctive of animals and plants have appeared in the course of the phylogenetic development of organisms, and were at first wanting. The simplest organisms, which now exist, are in all probability similar to those, which formed the starting-point of this development. The walls, which surround the elementary organs of the plant body, and the green colouring matter formed within them, have been cited as decisive indications of the vegetable character of an organism. Surrounded by firm walls, the living substance becomes more isolated, and, consequently, independence of action in plants, as compared with animals, is diminished. By means of the green colouring matter, plants have the power of producing their own nutritive substances from certain constituents of the air and water, and from the salts contained in the soil, and are thus able to exist independently; while animals are dependent for their nourishment, and so for their very existence, on plants. Almost all the other differences which distinguish plants from animals may be traced to the structure of plants, or to the manner in which they obtain their food. Another characteristic of plants is the unlimited duration of their ontogenetic development, which is continuous, at certain points at least, during their whole life. That none of these criteria are alone sufficient for distinguishing plants from animals is evident from the fact that all the Fungi are devoid of green pigment, and, like animals, are dependent on green plants for their nourishment. On the borderland of the two kingdoms, where all other distinctions are wanting, phylogenetic resemblances, according as they may indicate a probable relationship with plants or animals, serve as a guide in determining the position of an organism.

While it is thus difficult to sharply distinguish the two great groups of living organisms from one another, a distinction between them and lifeless bodies is readily recognised. Living organisms are endowed with the quality of IRRITABILITY, in which all lifeless bodies are deficient. External or internal stimuli influence living organisms to an activity, which is manifested in accordance with the requirements and conditions of their internal structure. Even in the smallest known organisms all manifestations of life are occasioned by a similar sensitiveness to external or internal stimuli. It is, therefore, probable that the simplest living beings must have possessed essentially simpler properties than any organisms now known, which would enable us to connect them with non-living substances. The substance which serves as a basis for all development must be supposed to have had an inorganic origin. On the other hand, it must not be forgotten that, so far as is actually known, all living organisms have arisen only from similar organisms. So far as experience has shown, spontaneous generation is unknown. In olden times it was a common supposition, which Aristotle himself held, that even highly organised animals and plants could originate from sand and mud. In the same degree that knowledge of the actual development of living organisms was extended, the previously accepted cases of spontaneous generation became more and more restricted, and were finally limited to intestinal worms which could not otherwise, it was thought, be accounted for, and to microscopic organisms, the origin of which also was not understood. Now, for such organisms the possibility of a spontaneous generation has been disproved by more modern investigations; the history of the development of intestinal worms is known, and the germs of organic life have been found to exist everywhere. Schwann and Pasteur have been pioneers in this work, and have shown that it is possible to hinder the development of the lower organisms, in places where it is customary to find them, by destroying all existing germs and at the same time preventing the entrance of new ones. It is due to the results obtained by these men in their investigations on spontaneous generation that we are now able to preserve food in a scientific manner. The germs previously existing in the substance to be conserved are destroyed by heat, while, by a proper mode of sealing, the entrance of new germs is rendered impossible, and the decomposition, which their presence would occasion, is accordingly prevented.

All known living organisms have been derived from other living organisms. But the idea of the origin of living from dead substances has on the other hand derived important support from the progress of chemical research. In the early decades of the last century it was customary to draw a distinct line of separation between organic and inorganic chemistry, and to assume that the substances dealt with by organic chemistry could only be produced by the vital action of organisms. The laws governing inorganic chemistry appeared to have no reference to organic chemistry, the formation of organic substance being due to a special force, the "life force." In 1828 Wöhler obtained urea from ammonium cyanate, and thus for the first time produced an organic compound from an inorganic substance. In 1845 Kolbe completely synthesised trichloracetic acid, and in 1850 Berthelot synthesised alcohol and formic acid. The former substance had been synthetically prepared by Hennel in 1828, but Berthelot was the first to recognise its identity with the substance formed in alcoholic fermentation. By these results the former distinction between organic and inorganic chemistry was destroyed. Organic chemistry has become the chemistry of carbon compounds.

In some such way it is possible that living matter originated from non-living at some period in the evolution of the earth when the conditions for its formation existed. In order that the organic world should have taken origin from the first living matter, one of the original properties of the latter must have been a capability of progressive development. It must have been capable of variation and of retaining the new characters appearing in this way, of growth, *i.e.* the increase of itself at the cost of foreign substances, and lastly, of reproduction, *i.e.* multiplication by separation into a number of parts.

Botany, or the science of plants, may be divided into a general and a special part. In the general part, the structure and functions of plants as such will be considered; in the special part, the particular structure and functions of the separate orders of plants will be discussed.

The study of the structure of plants is called Morphology; that of their functions Physiology. In the general part, morphology and physiology will be treated separately; in the special part, conjointly.

PART I

GENERAL BOTANY

SECTION I

MORPHOLOGY

GENERAL BOTANY

SECTION I

MORPHOLOGY

THE object of vegetable morphology is the scientific study of the forms of plants. It does not attempt to discover the causes of the variation in the forms, but rather has accomplished its purpose when it succeeds in showing how one form may be derived from another. The only real basis of morphological study is, accordingly, the genealogical development or phylogeny (p. 2). As phylogenetic development can only be inferred, and cannot be directly followed, the methods of morphology must also be indirect. They are dependent on the one hand upon ontogeny, *i.e.* on the study of the development passed through by an organism in attaining its mature condition, and on the other hand upon the comparison of existing organisms with one another and with those that have become extinct. To a certain extent the ontogenetic development of a plant repeats its phylogeny and helps to elucidate the latter, while, by means of comparative investigation, extreme forms may be connected by intermediate links. As, however, the ontogeny of a plant is neither an exact nor invariable repetition of its phylogeny, and as connecting links between extreme forms are often wanting, the results of morphological study are frequently imperfect and incomplete. Such parts or members of plants which it is reasonable to presume have had a common origin are distinguished as HOMOLOGOUS; those which, while probably having different origins, yet exercise the same functions, are termed ANALOGOUS. Through the adaptation of different parts to the same function, a similarity in both external form and internal structure often results; and in this way the correct determination of morphological relationships is rendered extremely difficult. Only homologous parts have the same morphological value. This homology is determined by the facts of phylogeny and origin, and not by any correspondence in function. On account, however, of the intimate relation existing between the form and function, and the modifying influence of the one upon the other, it will be necessary in the morphological study of the different members of plants to take into consideration their physiological signification, as organs. When, for phylogenetic reasons, it seems possible to attribute to a number of different members a common origin, such a hypothetical original form is termed the fundamental or primitive form ("Grundform"). The various modifications, which the primitive form has passed through, constitute its METAMORPHOSIS. In this way the theory of the metamorphosis of plants, which was once but an ideal conception, attains its true significance.

Slightly differentiated structures, which are found at the beginning of a series of progressively differentiating forms, are termed RUDIMENTARY; imperfect structures, which have arisen as the result of the deterioration of some perfect forms, are termed REDUCED.

Vegetable morphology includes the study of the external form and the internal structure of plants. The descriptive study of the external form of plants has been incorrectly termed ORGANOGRAPHY (7) for, by the use of the term "organ," it would seem to have a physiological signification. Morphology takes no recognition of the parts of a plant as organs, but treats of them merely as members of the plant body. On the other hand, one of the most important aims of physiology is to place the external form and the internal structure of the living body in relation to the functions performed by the latter; physiology also investigates the causes of the organisation. The study of the internal structure of plants is often designated ANATOMY or PHYTOTOMY; but as it usually includes also the study of the more minute internal structure, it resembles rather histology, in the sense in which that term is used by zoologists, and concerns itself to a much less degree with anatomy, properly speaking. In any case, it is the simplest plan to designate the study of the outer forms EXTERNAL MORPHOLOGY, and that of the inner structure INTERNAL MORPHOLOGY.

I. EXTERNAL MORPHOLOGY (8)

Plants show a great diversity in the form and arrangement of their members; it is the task of morphology to determine the points of agreement existing between them. To do this, it is necessary to discover a common origin for their similar but variously developed members.

The Development of Form in the Plant Kingdom

The Thallus.—When the body of a plant is not differentiated into separate members, or is composed of members, which (though they may be similar), are not homologous with those of the most highly organised plants, it is termed a THALLUS.

The simplest form that we can imagine for an organism is that of a sphere, and this is actually the form of some of the lower plants. The green growth often seen on damp walls consists of an aggregation of the small spherical bodies of *Gloeocapsa polydermatica* (Fig. 1), an Alga belonging to the lowest division of the vegetable kingdom. The single plants of the Beer-yeast (*Saccharomyces cerevisiae*) are ellipsoidal; but, from their peculiar manner of growth, by budding, they form lateral outgrowths, and thus often appear constricted (Fig. 2). Cylindrical and also disc-shaped forms are common to various Algae. The *Diatomeae* (Fig. 3), in particular, furnish a great variety of spindle, canoe, helmet, and fan-like shapes; but they may all be derived from the more simple spherical, discoidal, or cylindrical forms.

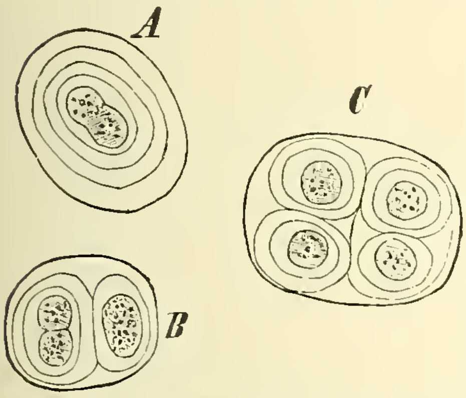


FIG. 1.—*Gloeocapsa polydermatica*. *A*, Commencement of division; *B*, shortly after division; *C*, a later stage. (× 540.)

FIG. 2.—*Saccharomyces cerevisiae*. 1, Cells without buds; 2 and 3, budding cells. (× 540.)

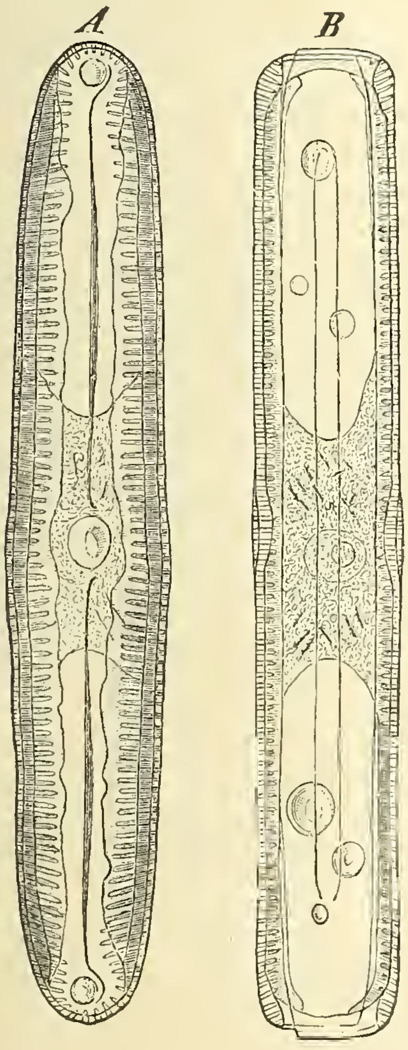


FIG. 3.—*Pinnularia viridis*. *A*, Surface view; *B*, lateral view. (× 540.)

FIG. 4.—Bacteria from deposits on teeth. *a*, *Leptothrix buccalis*; *a**, the same after treatment with iodine; *b*, *Micrococcus*; *c*, *Spirochaete dentium* after treatment with iodine; *d*, *Spirillum sputigenum*. (× 800.)

Among the *Bacteria*, which, as the cause of infectious diseases and of decomposition, have been the object of so much recent investigation, we also meet with spherical, rod-shaped, filamentous, and spirally wound forms (Fig. 4). The next stage in the progressive development of external form in the vegetable kingdom is exhibited by such plants as show a DIFFERENTIATION INTO APEX AND BASE. The base serves as a point of attachment, while growth is localised at the apex. In this way a growing point is developed at the apex. As an example of such a form, a young plant of the green Alga, *Ulva Lactuca* (Fig. 5), may be taken. The development of a more complicated external form is represented by the branched, filamentous, or band-shaped Algæ, in which the origin of new formations is more

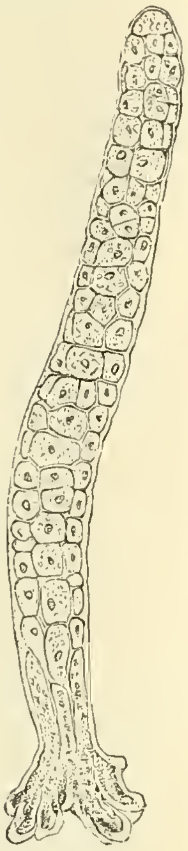


FIG. 5.—*Ulva Lactuca*, young stage, showing apex and base. (× 220.)

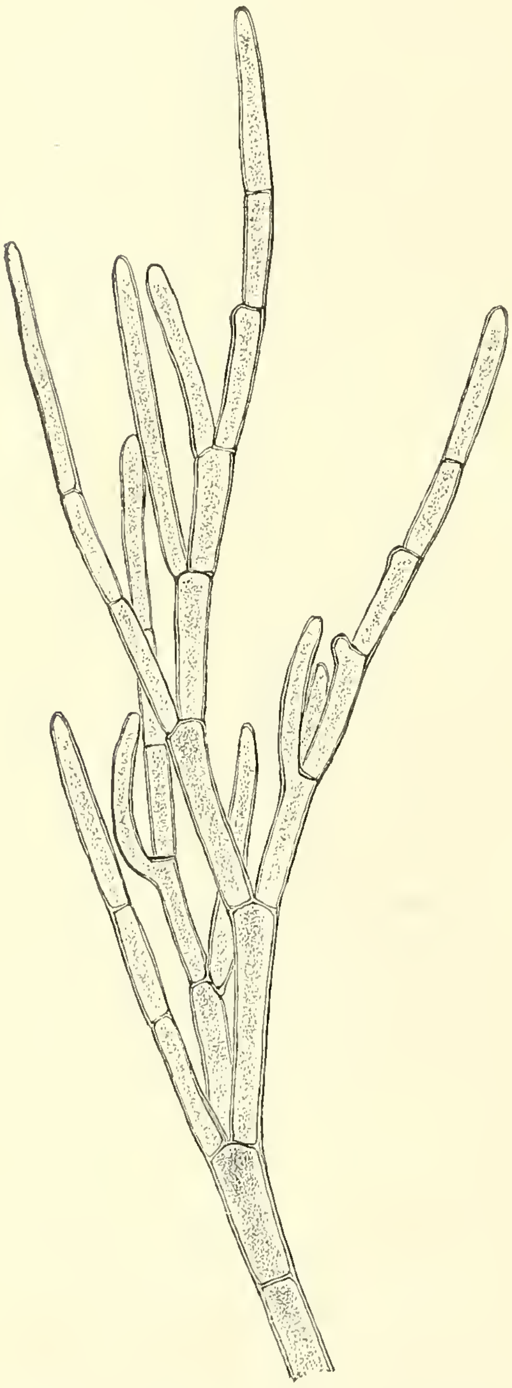


FIG. 6.—Portion of *Cladophora glomerata*. (× 48.)

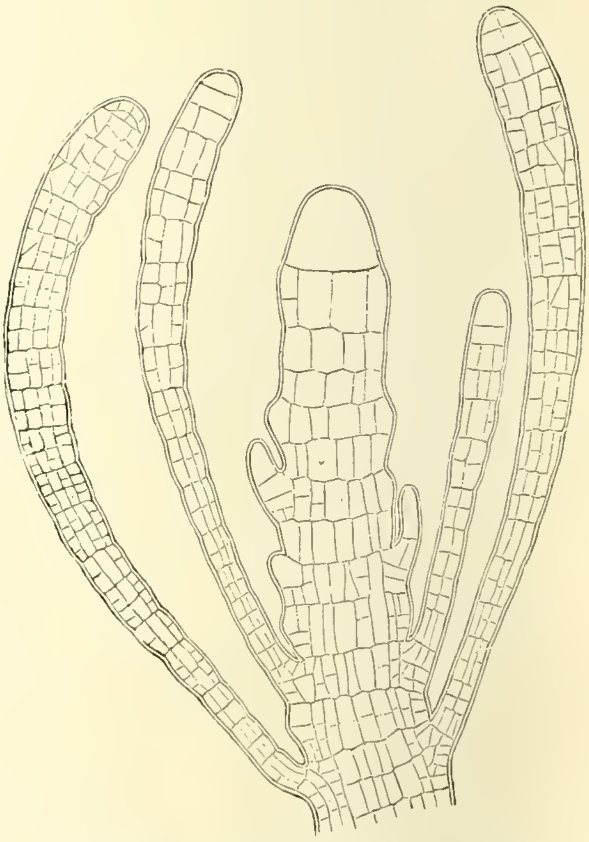


FIG. 7.—*Cladostephus verticillatus*. (After PRINGSHEIM, × 30.)

and more restricted to the apex. An ACROPETAL order of development, in which the youngest lateral members are always nearest the growing apex, is clearly demonstrated by the branched filaments of the common green Alga, *Cladophora glomerata* (Fig. 6). Still more pronounced is the apical growth in the brown sea-weed *Cladostephus verticillatus* (Fig. 7). The great variety in the form of the larger Fungi and Lichens, by which they are distinguished as club-, umbrella-, salver-, or bowl-shaped, or as bearded or shrub-like, is due to the union or intertwining of apically growing filaments. This manner of development is limited to Fungi and Lichens. In other cases, the more complete segmentation exhibited by the lower plants results from the differentiation of independently branching filaments and bands.

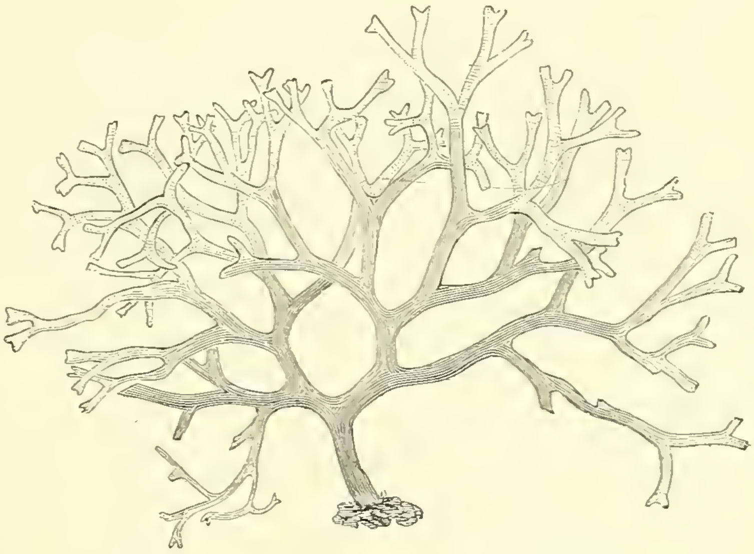


FIG. 8.—*Dictyota dichotoma*. ($\frac{2}{3}$ nat. size.)

As the apex itself may undergo successive modifications through continuous bifurcation, as in the case of *Dictyota dichotoma* (Fig. 8), it does not always necessarily follow that the formation of new members must proceed directly from the original apex. The highest degree of external differentiation among the lower plants is met with in certain groups of red and brown sea-weeds (*Rhodophyceae* and *Phaeophyceae*). Many representatives of these classes resemble the higher plants in the formation and arrangement of their members; *Hydrolapathum sanguineum* (Fig. 9), for example, as is indicated by its name, has a strong resemblance to a species of *Rumex*, and affords a remarkable illustration of the analogy of form existing between plants phylogenetically

FIG. 9.—*Hydrolapathum sanguineum*. ($\frac{1}{2}$ nat. size.)

unconnected. Since, however complicated its form in particular cases may be, the vegetative body of these lower plants is termed a THALLUS, they are collectively designated THALLOPHYTES. In contrast to the thallus, the body of the higher plants, with its segmentation into stem and leaves, is frequently termed a CORMUS, and the plants themselves CORMOPHYTES. To the Cormophytes belong all plants from the Ferns upwards.

Transition from the Thallus to the Cormus.—The lowest division of the Bryophytes, the Liverworts (*Hepaticae*), although in many cases possessing thalloid bodies without any segmentation into members, contain also forms with the same differentiation into stem and leaves as the higher plants. As between these two extremes there may be found transitional forms, this class of plants, accordingly, affords valuable assistance in the phylogenetic study of the development of cormophytic plants. A few examples will best illustrate these stages of differentiation exhibited by the *Hepaticae*. The bifurcately branching thallus of *Riccia fluitans* (Fig. 10) is flat and ribbon-like, and in its general appearance resembles the thallus of the previously mentioned brown Alga, *Dictyota dichotoma* (Fig. 8). A more advanced development is shown by *Blasia pusilla* (Fig. 11), which has incisions in the sides of its ribbon-like body. The lobes thus formed by the lateral incisions, as is shown by comparison with other more highly differentiated *Hepaticae*, and also by the study of their development, are properly to

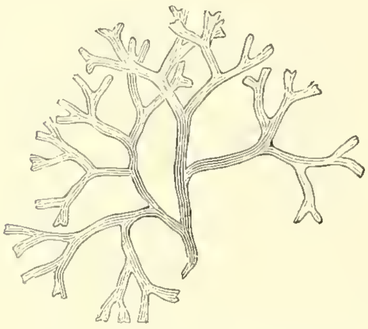


FIG. 10.—*Riccia fluitans*. (Nat. size.)

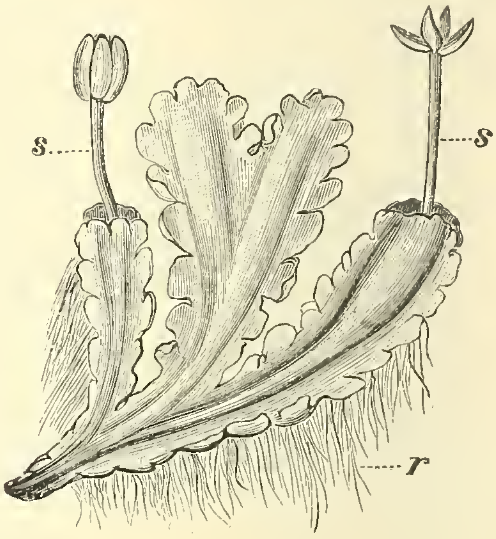


FIG. 11.—*Blasia pusilla*. *s*, Sporogonium; *r*, rhizoids. (× 2.)

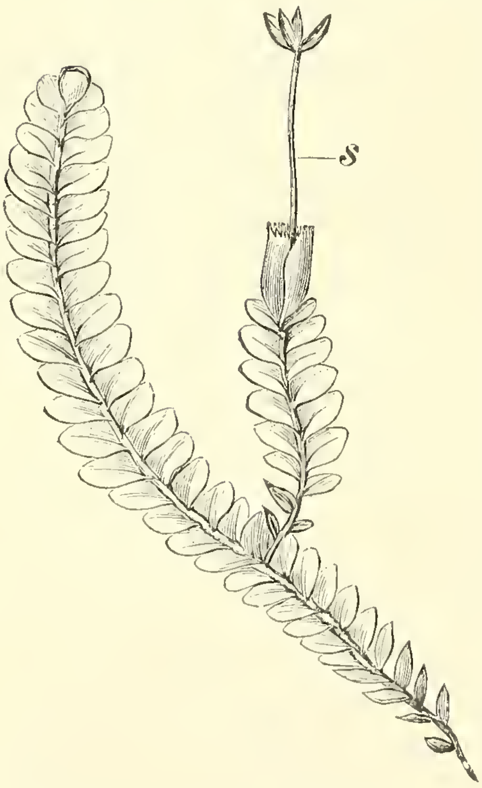


FIG. 12.—*Plagiochila asplenioides*. *s*, Sporogonium. (Nat. size.)

be regarded as leaves, the separation of which is still incomplete. Finally, in *Plagiochila asplenioides* (Fig. 12), with alternating ovate leaves and elongated fibrous stems, the segmentation into stem and leaf is complete.

The Cormus.—With the segmentation into stem and leaf, the distinctive differentiation of the Cormophyte is completed. This, in all probability, has occurred twice in the phylogenetic development of the vegetable kingdom; once in the Bryophytes, and a second time in the evolution of the Pteridophytes, probably in both cases from ancestral forms resembling the Liverworts. All Bryophytes are attached to the surface on which they grow, by means of slender filaments or RHIZOIDS (Fig. 11, *r*). It is in the next higher group of plants, which, as Pteridophyta or Vascular Cryptogams, are united in one class, that true roots, in a morphological sense, first make their appearance. They are for the most part cylindrical bodies with apical growing points. Disregarding the distinctions perceptible in its internal structure, a root may be distinguished from a stem by the ROOT-CAP or CALYPTRA sheathing its apex, and also by the absence of leaves.

The Metamorphosis of the Primitive Forms of Cormophytes.—After the completion of its differentiation into stem and leaf, and the appearance of roots, there occur only such modifications of the primitive form of the plant body of a Cormophyte as are embraced under its metamorphosis (p. 9), occasionally including a more or less complete fusion of parts originally separate and distinct.

The relationships between homologous members, which are often very striking, did not escape the notice of earlier observers. They suggested comparisons, although no real phylogenetic basis for such comparisons existed. Thus, an ideal conception of the form of external members was developed, and finally reached its highest elaboration in GOETHE's Theory of Metamorphosis; and its abstract scientific conclusion in the writings of ALEXANDER BRAUN. As the great variety exhibited in the external appearance of the lower plants precluded any possibility of assigning to them hypothetical primitive forms, the whole terminology of the external morphology of plants has been derived from conceptions applicable only to the Cormophytes. Even to-day, the same terms used in reference to the Cormophytes are applied to parts of the Thallophytes, which are evidently only analogous. In this sense it is customary to distinguish between stem and leaf in such Algæ as *Hydrolapathum* (Fig. 9). Such a use of terms is only permissible where reference is made to the manner of segmentation, with the intention of emphasising the analogy with the somewhat similar members of the Cormophytes. Indeed, even throughout the Cormophytes those structures designated by the same names are not truly homologous. For it is impossible to derive from the Bryophytes the forms of cormophytic segmentation shown by the Pteridophytes; the distinction into members appears to have originated independently in the two groups. As Goebel (9) has pointed out, leaves have appeared in several series of *Bryophyta*. However this may be, from the Pteridophytes upwards, the segmentation of the members appears to have had a similar origin, and the similarity of terminology is based, therefore, upon an actual homology of the parts.

Relations of Symmetry

Every section through an organ or member of a plant, made in the direction of its longitudinal axis, is distinguished as a longitudinal section; those at right angles to it being termed cross or transverse sections. Such parts of plants as may be divided by each of three or more longitudinal planes into like halves are termed either MULTILATERAL, RADIAL, or ACTINOMORPHIC. The degree of symmetry peculiar to any leafy shoot will be more apparent from a diagram, that is if the leaves which it bears be projected on a plane at right angles to its axis. The radial symmetry of a shoot with opposite leaves is clearly shown in the adjoining diagram (Fig. 13). A shoot with its leaves arranged alternately in two rows shows quite different relations of symmetry. The diagram of such a shoot (Fig. 14) can only be divided into similar halves by two planes. When such a condition exists, a member or plant is said to be BILATERAL or BISYMMETRICAL. When, however, a division into two similar halves is only possible in one plane, the degree of symmetry is indicated by the terms SIMPLY SYMMETRICAL, MONOSYMMETRICAL, or ZYGOMORPHIC; since, while the right and left halves correspond to one another, differences exist between the dorsal and ventral surfaces, such

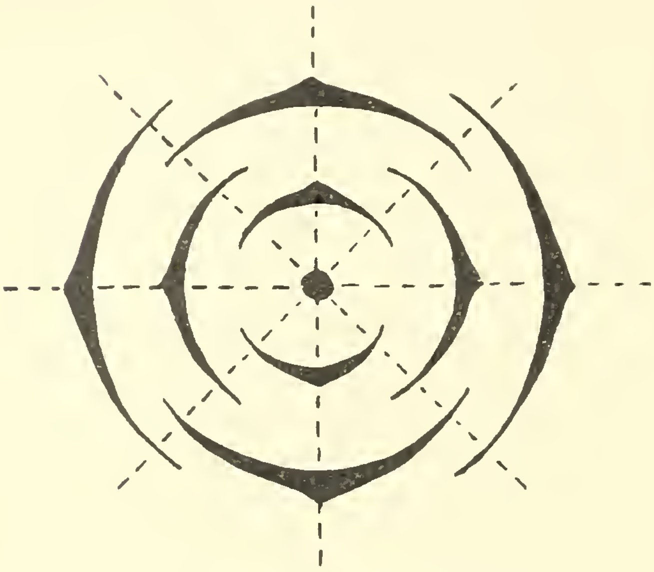


FIG. 13.—Diagram showing the so-called decussate arrangement of leaves.

FIG. 14.—Diagram showing two-ranked alternate arrangement of leaves.

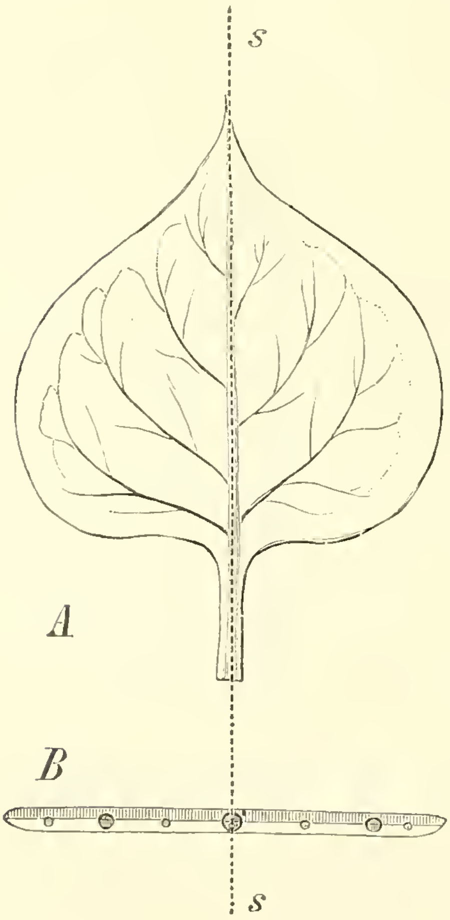


FIG. 15.—Diagram of a foliage-leaf. *A*, Surface view; *B*, transverse section; *s*, plane of symmetry.

bodies are also termed DORSIVENTRAL. Ordinary foliage-leaves exhibit this dorsiventral structure. In the accompanying figure (Fig. 15) such a monosymmetrical, dorsiventral foliage-leaf is diagrammatically represented. From the surface view (*A*) and from the cross-section (*B*), in which the distinction between the dorsal and ventral sides is indicated by shading, it is obvious that but one plane of symmetry (*s*) can be drawn. Dorsiventral members are often ASYMMETRICAL, not being divided by any plane into corresponding halves; the leaves of many kinds of *Begonia* will serve as examples of this.

Branch Systems

Thallophytes as well as Cormophytes exhibit systems of branching, resulting either from the formation of new growing points by the bifurcation of a previously existing growing point, or from the development of new growing points in addition to those already present. In this way there are produced two systems of branching, the DICHOTOMOUS and the MONOPODIAL. By the uniform development of a continuously bifurcating stem, a typical dichotomous system of branching is produced, such as is shown in *Dictyota dichotoma* (Fig. 8), and is represented diagrammatically in Fig. 16, *Aa*. In a typically developed example of the monopodial system there may always be distinguished

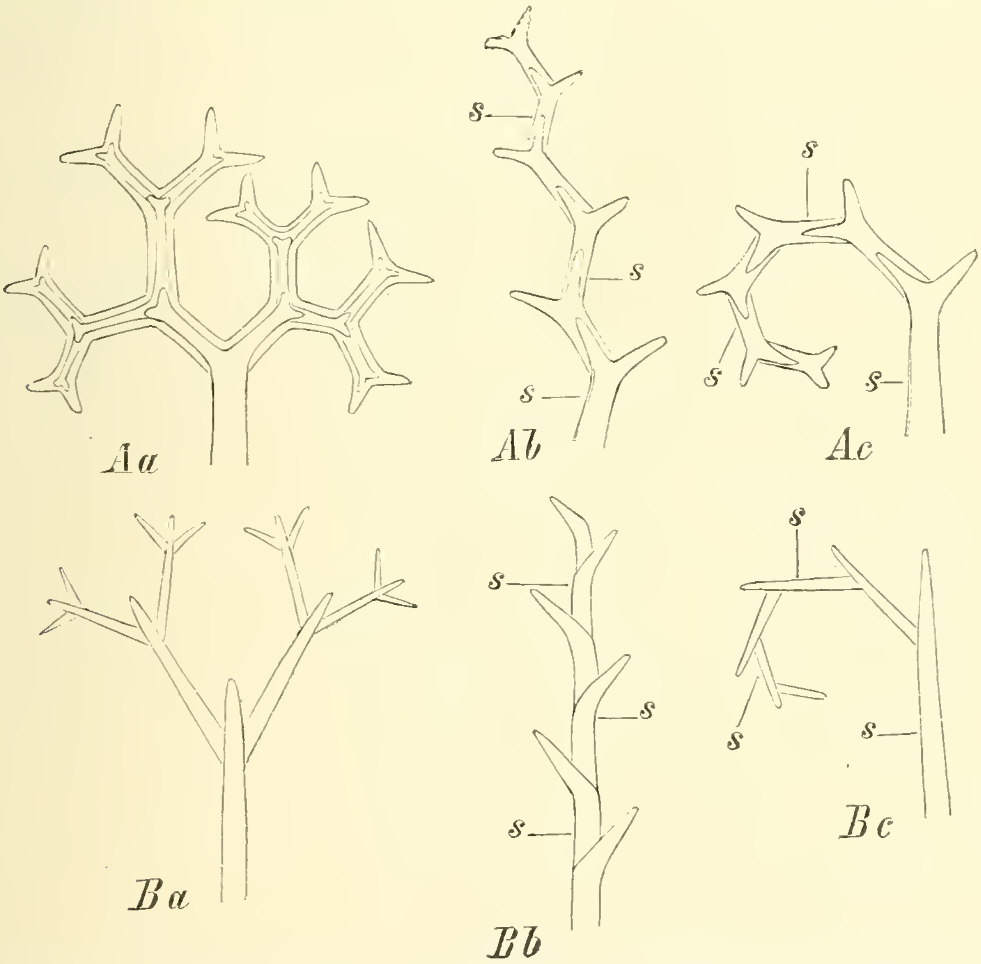


FIG. 16.—Diagrams of branch systems. *A*, Dichotomous branching; *Aa*, equal dichotomy; *Ab*, scorpioid dichotomy; *Ac*, helicoid dichotomy; *B*, monopodial branching; *Ba*, false dichotomy; *Bb*, scorpioid cyme; *Bc*, helicoid cyme; *ss*, sympodia.

a main axis, the MONOPODIUM, which gives rise to lateral branches from which, in turn, other lateral branches are developed. A good example of this form of branching is afforded by a Fir-tree. Where one of the two branches is regularly developed at the expense of the other, the dichotomous system assumes an appearance quite different from its typical form. The more vigorous branches may then, apparently, form a main axis, from which the weaker branches seem to spring, just as if they were lateral branches. This mode of branching (Fig. 16, *Ab*) is illustrated by the *Selaginellae.* Such an apparent main axis (*ss*) is termed, in accordance with its origin, a SYMPODIUM. On the other hand, in the monopodial system two or even several lateral branches may develop more strongly than the main axis, and so simulate true DICHOTOMY or POLYTOMY. Such monopodial forms of branching are referred to as FALSE DICHOTOMY (Fig. 16, *Ba*) or FALSE POLYTOMY, as the case may be. A good example of false dichotomy may be seen in the Mistletoe (*Viscum album*). If, however, a lateral branch so exceeds the main axis in development that it seems ultimately to become a prolongation of the axis itself, a sympodium is again formed (Fig. 16, *Bb*). This is exactly what occurs in the Lime and Beech; in both of these trees the terminal buds of each year's growth die, and the prolongation of the stem, in the following spring, is continued by a strong lateral bud, so that in a short time its sympodial origin is no longer recognisable. In most rhizomes, on the other hand, the sympodial nature of the axis can be easily distinguished; as, for example, in the rhizome of *Polygonatum multiflorum* (Fig. 23), in which, every year, the terminal bud gives rise to an aerial shoot, while an axillary bud provides for the continuance of the axis of the rhizome. In the flower-producing shoots or inflorescences of Phanerogams the different systems of branching assume very numerous forms. These will be more fully described in their proper place. To such inflorescences belong the ventrally coiled dorsiventral shoots, which produce new shoots from their convex dorsal surfaces, instead of in their leaf-axils.

The Shoot

The Development of the Shoot.—Under the term shoot a stem and its leaves are collectively included. A stem possesses an apical mode of growth (Fig. 17), and its unprotected growing point is described as naked, in contrast to that of the root with its sheathing root-cap. The apex of the shoot generally terminates in a conical protuberance, designated the VEGETATIVE CONE. As it is usually too small to be visible to the unaided eye, it is best seen in magnified median longitudinal sections. So long as the apex of the shoot is still internally undifferentiated, it continues in the embryonic condition, and it is from the still embryonal vegetative cone that the leaves take their origin.

They first appear in acropetal succession as small, conical protuberances, and attain a larger size the further removed they are from the apex of the stem. As the leaves usually grow more rapidly than the stem which produces them, they envelop the more rudimentary leaves, and overarching the vegetative cone, form, in this manner, a BUD. Buds are therefore merely undeveloped shoots. If they are to remain for a long time undeveloped, as for example is the case with winter buds, they are protected in a special manner during their period of rest.

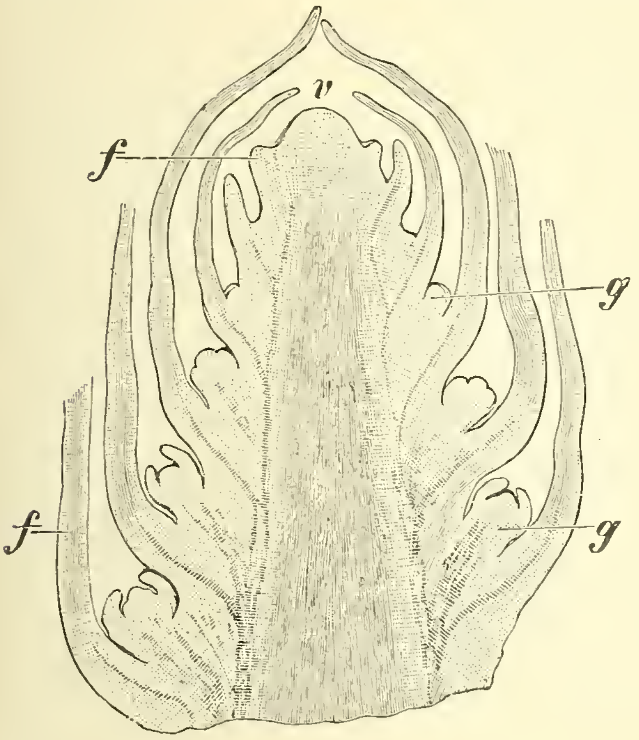


FIG. 17.—Apex of a shoot of a phanerogamic plant. *v*, Vegetative cone; *f*, leaf rudiment; *g*, rudiment of an axillary bud. (× 10.)

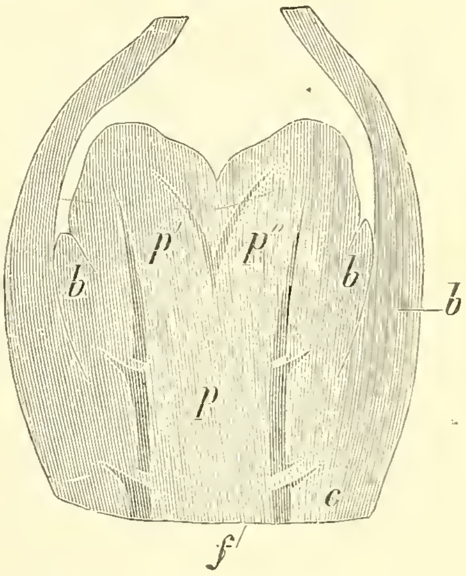


FIG. 18.—Longitudinal section of a bifurcating shoot (*p*) of *Lycopodium alpinum*, showing unequal development of the rudimentary shoots, *p'*, *p''*; *b*, leaf rudiments; *c*, cortex; *f*, vascular strands. (After HEGELMAIER, × 60.)

The Origin of New Shoots.—The formation of new growing points by the bifurcation of older points of growth, in a manner similar to that already described for *Dictyota dichotoma* (Fig. 8), occurs also, in almost typical form, in the lower thalloid *Hepaticae* (*Riccia fluitans*, Fig. 10). Among the Cormophytes this method of producing new shoots is of less frequent occurrence, and is then mainly limited to the Pteridophytes, for one division of which, the *Lycopodiaceae*, it is characteristic. In this case, whenever a shoot is in process of bifurcation, two new vegetative cones are formed by the division of the growing point (Fig. 18). In most of the *Lycopodiaceae* the new shoots thus formed develop unequally; the weaker becomes pushed to one side and ultimately appears as a lateral branch (Fig. 19). Although a relationship as regards position is generally apparent between

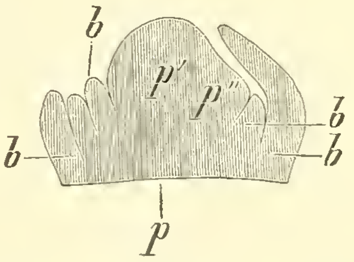


FIG. 19.—Bifurcating shoot (*p*) of *Lycopodium inundatum*, showing unequal development of the rudimentary shoots, *p'*, *p''*; *b*, leaf rudiments. (After HEGELMAIER, × 40.)

the origin of leaves and the lateral shoots, in the system of branching resulting from such a bifurcation of the vegetative cone this connection does not exist. In the more highly developed Bryophytes, particularly in the true Mosses, new shoots arise obliquely below the still rudimentary leaves at some distance from the growing point. In the Phanerogams new shoots generally arise in the axils of the leaves. In the accompanying illustration of a longitudinal section of a phanerogamic shoot (Fig. 17) the rudiment of a shoot (*g*) is just appearing in the axil of the third uppermost leaf; in the axils of the next older leaves the conical protuberances of the embryonic leaves are already beginning to appear on the still rudimentary shoot. These rudimentary shoots may either continue to develop, or they may remain for a time in an embryonic condition, as buds. Shoots thus produced in the axils of leaves are termed AXILLARY SHOOTS. The leaf, in the axil of which a shoot develops, is called its SUBTENDING LEAF. An axillary shoot is usually situated in a line with the middle of its subtending leaf, although it sometimes becomes pushed to one side. As a rule, only one shoot develops in the axil of a leaf, yet there are instances where it is followed by additional or ACCESSORY SHOOTS, which either stand over one another (serial buds), as in *Lonicera*, *Gleditschia*, *Gymnocladus*, or side by side (collateral buds), as in many *Liliaceae*.

Although in the vegetative regions, *i.e.* the regions in which merely vegetative organs are produced, the rudiments of the new shoots of phanerogamic plants make their appearance much later than those of the leaves, in the generative or flower-producing regions the formation of the shoots follows directly upon that of their subtending leaves, or it may even precede them. In this last case the subtending leaves are usually either poorly developed or completely suppressed, as in the inflorescence of the *Cruciferae*, in which a series of phylogenetic changes has probably led to this result.

Shoots developing in definite succession from the growing points of other shoots are designated NORMAL, in contrast to ADVENTITIOUS SHOOTS, which are produced irregularly from the older portions of a plant. Such adventitious shoots show no definite arrangement, and frequently spring from old stems, also from the roots of herbaceous plants (*Brassica oleracea*, *Anemone sylvestris*, *Convolvulus arvensis*, *Rumex Acetosella*), or of bushes (*Rubus*, *Rosa*, *Corylus*), or of trees (*Populus*, *Ulmus*, *Robinia*), or they may develop even from leaves, particularly from the fronds of Ferns. An injury to a plant will frequently induce the formation of adventitious shoots, and for this reason gardeners often make use of pieces of stems, rhizomes, or even leaves as cuttings from which to produce new plants. A leaf of a Begonia merely placed upon damp soil will soon give rise adventitiously to new plants.

Leaves and also normal shoots, which make their appearance as outgrowths from the portions of the parent shoot, still in embryonic condition, have an external or EXOGENOUS origin. Adventitious shoots, on the other hand, which arise from the older parts of stems or roots, are almost always ENDOGENOUS. They must penetrate the outer portions of their parent shoot before becoming visible. Adventitious shoots formed on leaves, however, arise, like normal shoots, exogenously.

The further Development of the Shoot.—All normal shoots are dependent for their origination upon the embryonic substance of the growing point of the parent shoot; even when they make their appearance at some distance from the growing apex (Fig. 17), embryonic substance has been reserved at that point for their formation. The growing points of adventitious shoots are also, for the most part, produced from tissue which has retained its embryonic condition in the older portions of the plant. In some cases, however, they arise from newly-developed growing points, and afford evidence of the power inherent in plants to return to an embryonic state and produce new growing points. The processes of development, which result in the production of new segments at the apex of a shoot, are followed by an increase in size and by the further growth of the segments. This growth is usually introduced by the vigorous elongation of the segments, by means of which their rapid unfolding from the bud is brought about. The region of strongest growth in a shoot is always at some distance from its growing point.

The growth in length and consequent elongation of the shoot is in some cases so slight that the leaves remain close together, and leave no free spaces on the stem, thus forming so called DWARF SHOOTS. As examples of such dwarf shoots may be mentioned the thickly-clustered needles or fascicled leaves of the Larch, the rosettes formed by the fleshy leaves of the House-leek (*Sempervivum*), and also the flowers of Phanerogams with their thickly-crowded floral leaves. In the ordinary or ELONGATED SHOOTS, such as are formed in the spring by most deciduous trees, the portions of the stem between the insertions of the leaves become elongated by the stretching of the shoot. The stem of a shoot, as contrasted with the leaves, is often spoken of as the axis; the portions of the stem axis between the insertions of the leaves are termed the INTERNODES, and the parts of the axis, from which the leaves arise, the NODES. When the base of the leaves encircles the stem, or when several leaves take their origin at the same node, the nodes become strongly marked (*Labiatae*).

In some cases the growth in length of a shoot continues for a longer time at certain intermediate points by means of INTERCALARY GROWTH. Such points of intercalary growth are generally situated at the base of the internodes, as in the case of the Grasses. A displacement from the position originally occupied by the members of a shoot frequently results from intercalary growth. A bud may thus, for example, become pushed out of the axil of its subtending leaf, and so apparently have its origin much higher on the stem; or a subtending leaf, in the course of its growth, may carry its axillary bud along with it, so that the shoot which afterwards develops seems to spring directly from its subtending leaf; or, finally, the subtending leaf may become attached to its axillary shoot, and growing out with it, may thus appear to spring from it (Fig. 20).

Fig. 20.—*Samolus Valerandi*, each axillary shoot (*a*) bearing its subtending leaf (*t*), and terminating in a fruit. (Nat. size.)

Resting Buds.—As a means of protection, buds (Fig. 21) may become invested, in winter, with scale-like leaves or BUD-SCALES, which are rendered still more effective as protective structures by hairy outgrowths and excretions of resin and gum, and also by the occurrence of air-spaces. Not infrequently the subtending leaf takes part in the protection of its axillary bud, and the base of the leaf-stalk, after the leaf itself has fallen, remains on the shoot and forms a cap-like covering for the winter bud. The buds of tropical plants, which have to withstand a dry period, are similarly protected; but where the rainfall is evenly distributed throughout the year buds develop no such means of protection.

All the buds of a plant do not develop; there are numerous deciduous trees—such as the Willow, in which the terminal buds of the year's growth regularly die. Sometimes buds, usually the first-formed buds of each year's shoot, seem able to remain dormant during many years without losing their vitality; these are termed DORMANT BUDS. In the case of the Oak or Beech such latent buds can endure for hundreds of years; in the meantime, by the elongation of their connection with the stem, they continue on its surface. Often it is these, rather than adventitious buds, which give rise to the new growths formed on older parts of stems. It may sometimes happen that the latent buds lose their connection with the woody parts of their parent stem, but nevertheless grow in thickness, and develop their own wood; they then form remarkable spherical growths within the bark, which may attain the size of a hen's egg and can be easily separated from the surrounding bark. Such globular shoots are frequently found in Beech and Olive trees.

Fig. 21.—Winter buds of the Beech (*Fagus silvatica*). *kns*, Bud-scales. (Nat. size.)

The Metamorphosis of the Bud.—The BULBILS and GEMMÆ, which become separated from their parent plant and serve as a means of reproduction, are special forms of modified buds. They are always well supplied with nutritive substances, and are of a corresponding size. Many plants owe their specific name to the fact that they produce such bulbils, as, for example, *Lilium bulbiferum* and *Dentaria bulbifera* (Fig. 22).

The Metamorphosis of Subterranean Shoots.—Shoots that live underground undergo characteristic modifications, and are then termed ROOT-STOCKS or RHIZOMES. By means of such subterranean shoots many perennial plants are enabled to persist through the winter. A rhizome develops only reduced leaves in the form of larger or smaller, sometimes scarcely visible, scales. By the presence of such scale leaves, with their axillary buds, and by its naked vegetative cone, as well as by its internal structure, a rhizome may be distinguished from a root. Rhizomes usually produce numerous roots; but when this is not the case, the rhizome itself functions as a root. Rhizomes often attain a considerable thickness and store up nutritive material for the formation of aerial shoots. In the accompanying illustration (Fig. 23) is shown the root-stock of the so-called Solomon's Seal (*Polygonatum multiflorum*). At *d* and *c* are seen the scars of the aerial shoots of the two preceding years; and at *b* may be seen the base of the stem growing at the time the rhizome was taken from the ground, while at *a* is shown the bud of the next year's aerial growth. The rhizome of *Coralliorrhiza innata*, a saprophytic Orchid, affords a good example of a root-stock functioning as a root (Fig. 24). BULBS, also, belong to the

FIG. 22.—Shoot of *Dentaria bulbifera*, bearing bulbils, *br*. (Nat. size.)

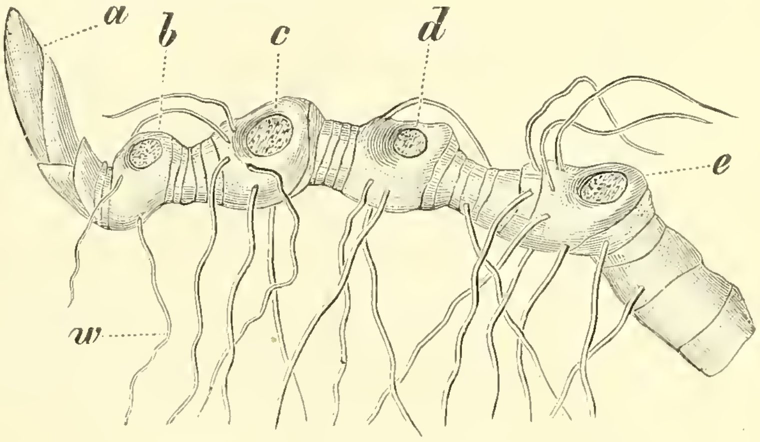


FIG. 23.—Rhizome of *Polygonatum multiflorum*. *a*, Bud of next year's aerial growth; *b*, scar of this year's, and *c*, *d*, *e*, scars of three preceding years' aerial growth; *w*, roots. ($\frac{3}{4}$ nat. size.)

class of metamorphosed shoots. They represent a shortened shoot with a flattened, discoid stem (Fig. 25, *zk*), the fleshy thickened scale leaves (*zs*) of which are filled with reserve food material. The aerial growth of a bulb develops from its axis, while new bulbs are formed from buds (*k*) in the axils of the scale leaves. Another form of underground shoot, allied to bulbs and connected with them by transitional forms, is distinguished as a TUBER. The axis of a typical tuber, in contrast to that of a bulb, is fleshy and swollen, serving as a reservoir of reserve material, while the leaves are thin and scaly. Of such tubers those of the Meadow Saffron (*Colchicum autumnale*) or of *Crocus sativus* are good examples. In the Meadow Saffron new tubers arise from axillary buds near the base of the modified shoot, but in the Crocus from buds near the apex. In consequence of this, in the one case the new tubers appear to grow out of the side, and in the other to spring from the top of the old tubers. The tubers of the Potato (Fig. 26) or of the Jerusalem Artichoke (*Helianthus tuberosus*) are also subterranean shoots with swollen axes and reduced leaves. They are formed from the ends of branched, underground shoots or runners (STOLONS) and thus develop at a little distance from the parent plant. The so-called eyes on the outside of a potato, from which the next

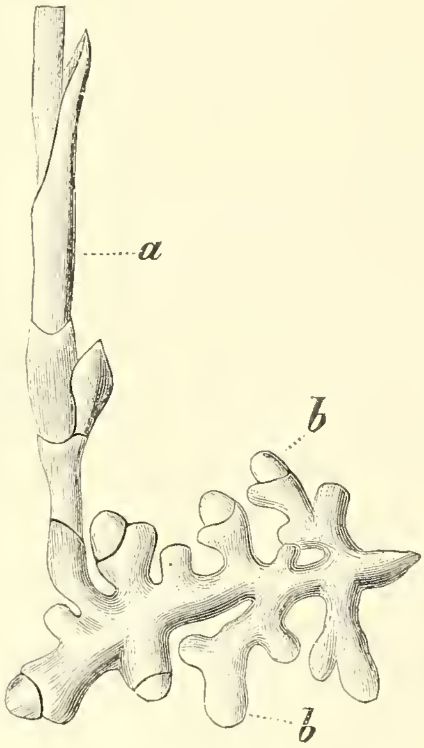


FIG. 24.—Rhizome of *Coralliorrhiza innata*. *a*, Floral shoot; *b*, rudiments of new rhizome branches. (After SCHACHT, nat. size.)

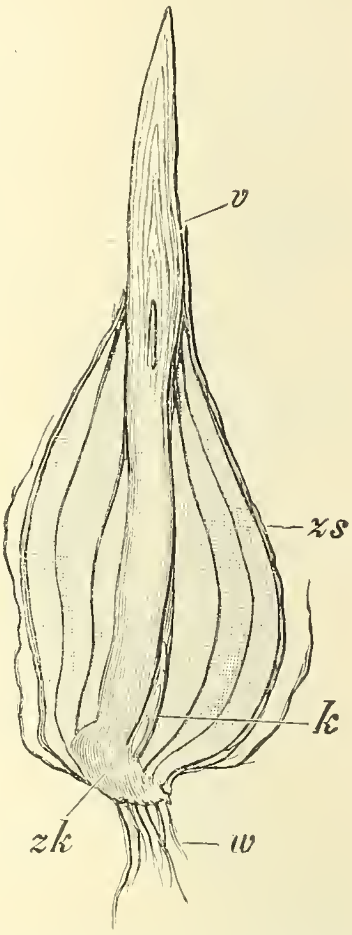


FIG. 25.—Longitudinal section of tulip bulb, *Tulipa Gesneriana*. *zk*, Modified stem; *zs*, scale leaves; *v*, terminal bud; *k*, rudiment of a young bulb; *w*, roots. (Nat. size.)

year's growth arises, are in reality axillary buds, but the scales which represent their subtending leaves can only be distinguished on very young tubers. The parent plant dies after the formation of the tubers, and the reserve food stored in the tubers nourishes the young plants which afterwards develop from the eyes. As, in their uncultivated state, the tubers of the Potato plant remain in the ground and give rise to a large number of new plants, it is of great advantage to the new generation that the tubers are produced at the ends of runners, and are thus separated from one another.

The Metamorphosis of Aerial Shoots.—Similar advantages to those obtained by the elongation of the underground shoots in the Potato accrue from surface runners, such as are produced on Strawberry plants. Surface runners also bear scale-like leaves with axillary buds, while roots are developed from the nodes. The new plantlets, which arise from the axillary buds, ultimately form independent plants by the death of the intervening portions of the runners.

FIG. 26.—Part of a growing Potato plant, *Solanum tuberosum*. The whole plant has been developed from the dark-coloured tuber in the centre. (From Nature, copied from one of BAILLON's illustrations, ⅓ nat. size.)

Still more marked is the modification experienced by shoots which only develop reduced leaves, but the axes of which become flat and leaf-like, and assume the functions of leaves. Such leaf-like shoots are called CLADODES or PHYLLOCLADES. Instructive examples of such formations are furnished by *Ruscus aculeatus* (Fig. 27), a small shrub whose stems bear in the axils of their scale-like leaves (*f*) broad, sharp-pointed cladodes (*cl*), which have altogether the appearance of leaves. The flowers arise from the upper surface of these cladodes, in the axils of scale leaves. In like manner the stems of the Opuntias (Fig. 28) are considerably flattened, while the leaves are reduced to small thorny protuberances. In this case the juicy flat shoots perform not only the functions of assimilatory organs, but also serve as water-reservoirs in time of drought. It is possible that all the leaves of a plant may become more or less completely reduced, without any marked change occurring in the appearance of the stems, except that they then take on a green colour; this, for example, is the case in the Scotch Broom (*Spartium scoparium*), which develops only a few quickly-falling leaves on its long, naked twigs. As a rule, however, leafless green Phanerogams will be found to have swollen stems, as in the variously shaped *Euphorbiae* and *Cacti*.

FIG. 27.—Twig of *Ruscus aculeatus*. *f*, Leaf; *cl*, cladode; *bl*, flower. (Nat. size.)

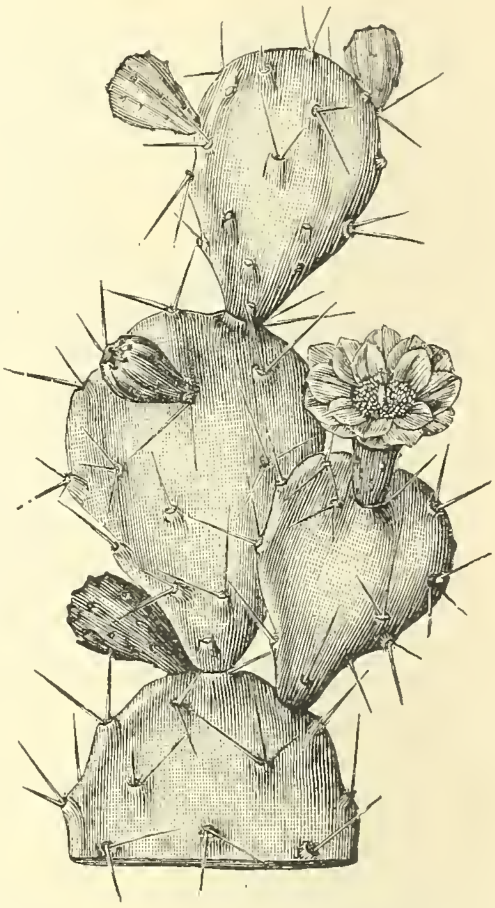


FIG. 28.—*Opuntia monacantha* Haw., showing flower and fruit. (After SCHUMANN, ⅛ nat. size.)

Reduction of the Shoot in Parasites.—A great reduction in the leaves, and also in the stems, often occurs in phanerogamic parasites, in consequence of their parasitic mode of life. The leaves of the Dodder (*Cuscuta*, Fig. 186, *b*) are only represented by very small, yellowish scales, and the stem is similarly yellow instead of green. The green colour would, in fact, be superfluous, as the Dodder does not produce its own nourishment, but derives it from its host plant. *Cuscuta Trifolii*, one of the most frequent of these parasites, is often the cause of the large yellow areas frequently observable in the midst of clover fields. In certain tropical parasites belonging to the family

Rafflesiaceae, the process of reduction has advanced so far that the flowers alone are left to represent the whole plant. *Rafflesia Arnoldi*, a plant growing in Sumatra, is a remarkable example of this; its flowers, although they are a metre wide, the largest flowers in existence, spring directly from the roots of another plant (species of *Cissus*).

Tendrillar Shoots.—A peculiar form of metamorphosis is exhibited by some climbing plants through the transformation of certain of their shoots into TENDRILS. Such tendrils assist the parent plant in climbing, either by twining about a support or otherwise holding fast to it. The twining bifurcated tendrils of the Grape-vine, for example, are modified shoots, and so are also the more profusely branched, hold-fast tendrils of *Ampelopsis Veitchii* (Fig. 29).

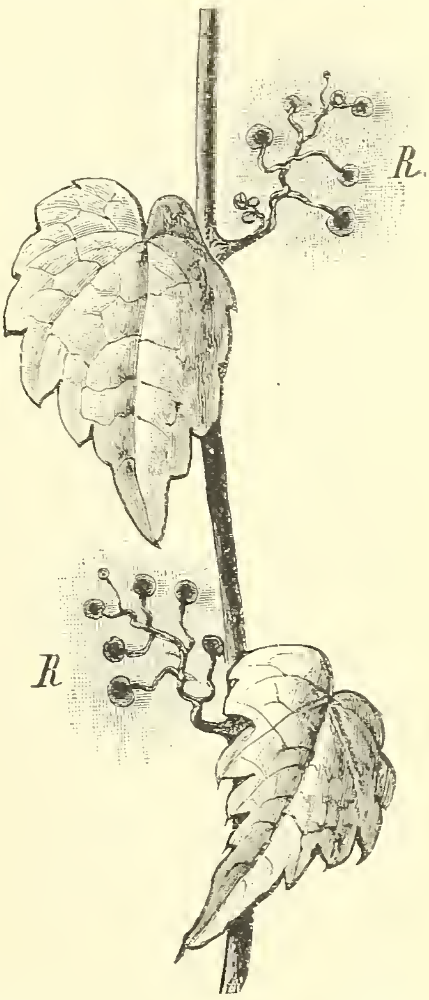


FIG. 29.—*Ampelopsis Veitchii*. *R*, *R*, Stem-tendrils. ($\frac{3}{4}$ nat. size.)

Stem-thorns.—Shoots may undergo a still greater reduction by their modification into THORNS, as a defence against the depredations of animals. Of shoots modified in this manner, the Black Thorn (*Prunus spinosa*), the White Thorn (*Crataegus*), and the Honey Locust (*Gleditschia*) afford instructive examples. The thorns are simple or branched, hard, pointed bodies. In *Gleditschia* (Fig. 30) the thorns are developed primarily from the uppermost of several serial buds; while secondary thorns may develop on older portions of the stem from the lower buds of the series, and thus give rise to clusters of thorns. In *Colletia cruciata* all the shoots are flattened and spiny, so that they perform the duties of leaves in addition to serving as protective structures. This plant is an American shrub belonging to the *Rhamnaceae*, which grows in dry sunny situations.

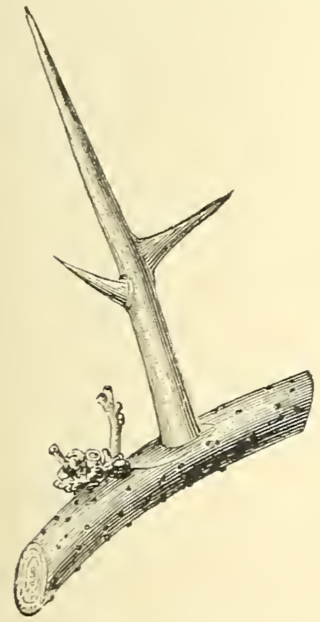


FIG. 30.—Stem-thorn of *Gleditschia triacanthos*. ($\frac{1}{2}$ nat. size.)

Flowers.—The most marked changes in the form of the shoot, due to the displacement and union of its different members, take place in phanerogamic flowers. The shoots from which flowers are developed are termed FLORAL SHOOTS, in contrast to the FOLIAGE SHOOTS, the functions of which are merely vegetative. The axis of the floral shoot remains short and becomes flattened or even depressed at the tip.

The leaves which spring from the floral axis often become united with one another and with the axis itself. In such cases thorough investigation of the development and the comparative morphology of the flower is necessary to reveal the modifications which have taken place during its evolution. In most instances the rule seems to hold that axillary buds are not formed within a flower except in cases of abnormal development.

The Order of Sequence of Shoots.—If the vegetative cone of the primary axis of a plant, after reaching maturity, is capable of reproduction, a plant with but one axis will result, and the plant is designated UNIAXIAL or haplocaulescent. Usually, however, it is not until a plant has acquired axes of the second or third order, when it is said to be DIPLOCAULESCENT or TRIPLOCAULESCENT, or of the *n*th order, that the capacity for reproduction is attained. A good illustration of a plant with a single axis is afforded by the Poppy, in which the first shoot produced from the embryo terminates in a flower, that is, in that organ of Phanerogams which includes the sexual organs. As an example of a plant with a triple axis may be cited the common Plantain, *Plantago major*, whose primary axis produces only foliage and scale leaves; while the secondary axes give rise solely to bracteal leaves, from the axils of which finally spring the axes of the third order, which terminate in the flowers. In the case of trees, only shoots of the *n*th order can produce flowers. Thus a division of labour commonly occurs in a branched plant, which finds its expression in differences of form between the successive shoots. These differ in appearance according to the special function performed by them, whether nutrition, storage, or reproduction. In addition to the essential members in the succession of shoots developed in a determined order, there are non-essential members which repeat forms of shoot already present. These may appear simultaneously with the essential shoots, and serve to increase the size of the plant as in many annuals; in many perennial plants they arise as yearly innovations on the stock. Adventitious shoots, as a rule, repeat members which have already made their appearance. Exceptionally, they form necessary links in the succession of shoots; this is the case in the *Podostemaceae*, an aquatic order of Dicotyledons found in the tropics, the plants belonging to which resemble Liverworts in external form.

The Habit or General Aspect of Plants is dependent upon the origin, number, mode of growth, and duration of their branches, and on the presence or absence of non-essential shoots. Cormophytes which develop herbaceous aerial shoots, and persist only so long as is requisite for the development and ripening of their fruit, be it one or several vegetative periods, are called HERBS. Herbaceous plants, however, which, although annually dying down to the ground, renew their existence each year by means of new shoots produced from underground shoots, rhizomes, or roots, are further distinguished as

PERENNIALS or perennial herbs. SHRUBS or TREES, on the other hand, have woody, persistent shoots, which bear fruit repeatedly. In these the reproductive shoots are shed annually, and, in some, vegetative branches are also cast off, the remaining ones persisting and increasing in thickness. In the Lime the ends of the leafy twigs, in the Scotch Fir the short shoots, and in the Oak, Elm, Willow, and Poplar weak lateral branches are thus lost. The leaves of evergreen trees remain alive for several years, while those of deciduous species only persist for a single vegetative period.

Shrubs retain their lateral shoots, so that their branches are formed near the ground; trees, on the contrary, soon lose their lower lateral branches, and have a main stem or trunk, which bears a crown of branches and twigs. In many trees, shrubs, and herbs the main shoot is vertical, while the lateral branches assume a horizontal position, or are directed obliquely upwards or downwards. In other cases the main axis is sympodial, a lateral branch continuing the direction of growth of the primary shoot. Sometimes a main axis is indistinguishable among the group of similarly directed branches. The general appearance of the plant is determined by the direction and thickness of its branches and leafy twigs. If these are all directed upwards the shape is pyramidal, while broadly pyramidal, oval, and rounded forms arise when the branches diverge more strongly. The "weeping varieties" of several familiar trees, due to the branches becoming long and pendulous, afford a good illustration of the dependence of habit upon the mode of branching. Herbaceous plants often have stems which creep on the surface of the ground, while other plants climb upon various supports by means of hooked hairs, tendrils, and winding movements. The latter are called climbing plants, or, if their stems are woody, lianes. It is the presence of numerous rope-like stems of lianes which renders the tropical forest so impenetrable. On both creeping and climbing shoots the leaves tend to become displaced towards the dorsal surface of the stem, while branches spring from the sides and roots from the ventral surface.

In catalogues and descriptions of plants the duration of the period of growth is usually expressed by special symbols: thus ⊙ indicates an annual; ⚇ a biennial, and ♃ a perennial herb; ♄ is employed to designate both trees and shrubs, and for trees the sign ♄ is also in use.

The Leaf

Development of the Leaf.—The first appearance of the leaf as a lateral protuberance (Fig. 17, *f*) on the vegetative cone of the shoot has already been referred to (p. 18). When the apex of a shoot is removed by a transverse section and viewed from above (Fig. 31), the origin of leaves as lateral protuberances is more evident than in a longitudinal section. The embryonic leaf rudiment generally occupies but a small portion of the periphery of the vegetative cone; it may, however, completely invest it. In like manner, when the mature leaves are arranged in whorls, the developing protuberances of the rudimentary leaves may, although this is not usually the case, form at first a continuous wall-like ring around the growing point; and only give rise later to the separate leaf rudiments. Leaves take their origin only from such parts of a plant as have remained in an embryonic condition. To this rule there are no exceptions. A leaf never arises directly from the older parts of a plant. In cases where it apparently does so its development has been preceded by the formation of a growing point of a new shoot. When it first appears on the vegetative cone a rudimentary leaf resembles an embryonic shoot, but a difference soon manifests itself, and the shoot rudiment develops a vegetative cone and lateral protuberances for the formation of leaves. The growing point of a shoot has usually an UNLIMITED GROWTH, while the growth of a leaf is LIMITED. A leaf usually continues to grow at its apex for a short time only, and then completes its segmentation and development by intercalary growth, which is usually localised near the base. It is true that some leaves, as those of Ferns, not only continue growing for a long time, but also retain a continuous apical growth and complete their whole segmentation in acropetal succession. On the other hand, the leaf-like cladodes, although they are in reality metamorphosed shoots, exhibit a limited apical growth like that of ordinary leaves.

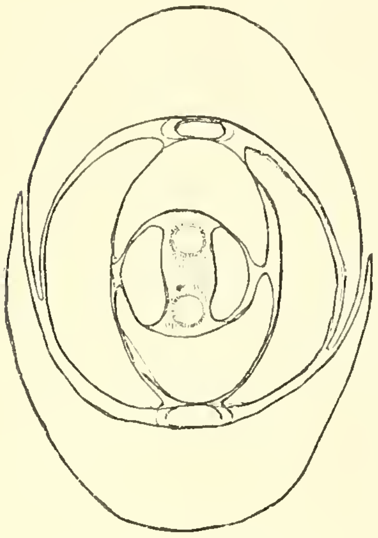


Fig. 31.—Apical view of the vegetative cone of a shoot of *Evonymus japonicus*. (× 12.)

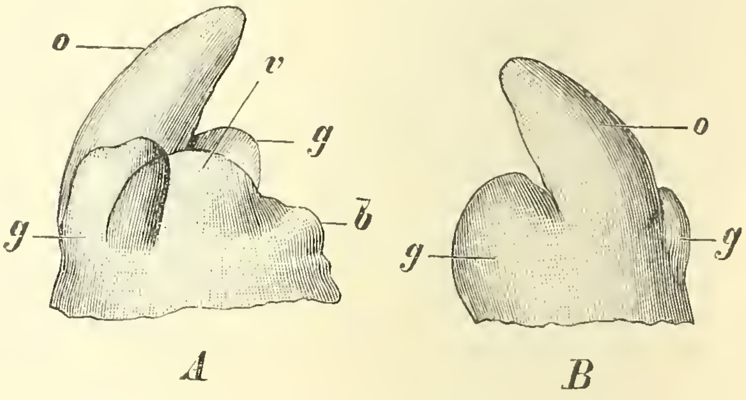


Fig. 32.—Apex of an Elm shoot, *Ulmus campestris*. *A*, Showing the vegetative cone *v*, with the rudiments of a young leaf, *b*, still unsegmented, and of the next older leaf, exhibiting segmentation into the laminar rudiment, *o*, and leaf-base, *g*; *B*, showing the older leaf, viewed from the side. (× 58.)

Leaving out of consideration the Ferns and a few related plants, the following observations in regard to the development of the leaf hold good for the majority of Cormophytes. The unsegmented protuberance of the still rudimentary leaf, termed by Eichler (10) the PRIMORDIAL LEAF (Fig. 32, *A*, *b*), first projects from the vegetative cone of the shoot (*A*, *v*). This is usually followed by a separation of the primordial leaf into the LEAF-BASE (*g* in *A* and *B*) and the rudimentary lamina or UPPER LEAF (*o* in *A* and *B*). The leaf-base, or the part of the rudimentary leaf which immediately adjoins the vegetative cone, either takes no further part in the succeeding differentiation of the leaf, or it develops into a LEAF-SHEATH (vagina) or into STIPULES. The upper leaf, on the other hand, gives rise to the leaf-blade or LAMINA. If the fully-developed leaf possesses a LEAF-STALK (petiole), it becomes afterwards interposed by intercalary growth between the upper leaf and the leaf-base.

The Metamorphosis of the Leaf is exhibited in its greatest diversity by the leaves of Phanerogams, in which the various homologous leaf structures have been distinguished as SCALE LEAVES, FOLIAGE LEAVES, BRACTEAL LEAVES, and FLORAL LEAVES (Fig. 33).

Foliage Leaves, generally referred to simply as leaves, are the leaf structures on which devolves the task of providing nourishment for their parent plants. As the exercise of this function is dependent upon the presence of a green pigment, foliage leaves have, accordingly, a green colour. In certain cases, where their form is extremely simple, as in the needles of Conifers, the primordial leaf simply increases in length without any further differentiation into parts. In other undivided leaves, however, whether lanceolate, elliptical, ovate, or otherwise shaped, the flat leaf-blade is distinct from the leaf-base, while a leaf-stalk may also be interpolated between them. If no leaf-stalk is developed the leaf is said to be SESSILE, otherwise it is described as STALKED. The sessile leaves usually clasp the stem by a broad base. Where, as in the case of the Poppy (*Papaver somniferum*), the leaf-base surrounds the stem, the leaves are described as AMPLEXICAUL; if, as in species of *Bupleurum*, it completely surrounds the stem, the term

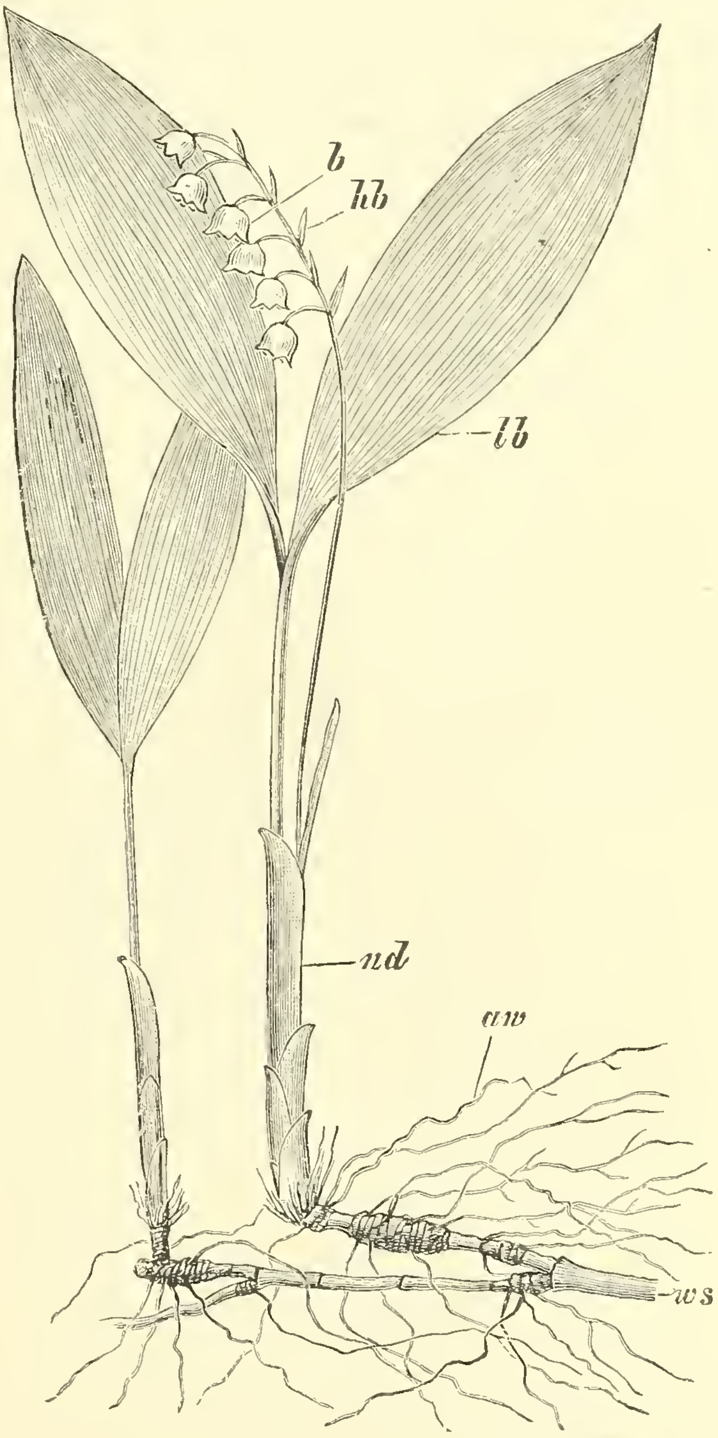


FIG. 33.—Lily of the Valley (*Convallaria majalis*). *nd*, Scale leaves; *lb*, foliage leaves; *hb*, bracts; *b*, flower; *ws*, rhizome; *aw*, adventitious roots. (Slightly reduced.)

PERFOLIATE is used. If the bases of two opposite leaves have grown together, as in the Honeysuckle (*Lonicera Caprifolium*), they are said to be CONNATE. Where the blade of the leaf continues downwards along the stem, as in the winged stems of the common Mullein (*Verbascum thapsiforme*), the leaves are distinguished as DECURRENT. The petiole of a leaf merges either directly into the leaf-base, or it swells at its lower end into a LEAF-CUSHION or PULVINUS, and is thus articulated with the leaf-base. This is the case, for instance, with many of the *Leguminosae* (Fig. 214). The leaf-blade, in turn, may be either sharply marked off from the petiole, or it may be prolonged so that the petiole appears winged, or again it may expand at its junction with the petiole into ear-like lobes. A leaf is said to be ENTIRE if the margin of the leaf-blade is wholly free from indentations; otherwise, if only slightly indented, it is usually described as SERRATE, DENTATE, CRENATE, UNDULATE, SINUATE, or INCISED, as the case may be. When the incisions are deeper, but do not extend more than half-way to the middle of the leaf-blade, a leaf is distinguished as LOBED or CLEFT according to the character of the incisions, whether more or less rounded or sharp; if the incisions are still deeper the leaf is said to be PARTITE, and if they penetrate to the midrib or base of the leaf-blade it is termed DIVIDED. The divisions of the leaf-blade are said to be PINNATE or PALMATE, according as the incisions run towards the midrib or towards the base of the leaf-blade. Where the divisions of the leaf-blade are distinct and have a separate insertion on the common leaf-stalk or on the midrib, then termed the SPINDLE or RHACHIS, a leaf is spoken of as COMPOUND (Fig. 34, *ub*); in all other cases it is said to be SIMPLE. The single, separate divisions of a compound leaf are called leaflets. These leaflets, in turn, may be entire, or may be divided and undergo the same segmentation as single leaves. In this way double and triple compound leaves may be formed. The leaflets are either sessile or stalked; and sometimes also, as in *Robinia* and

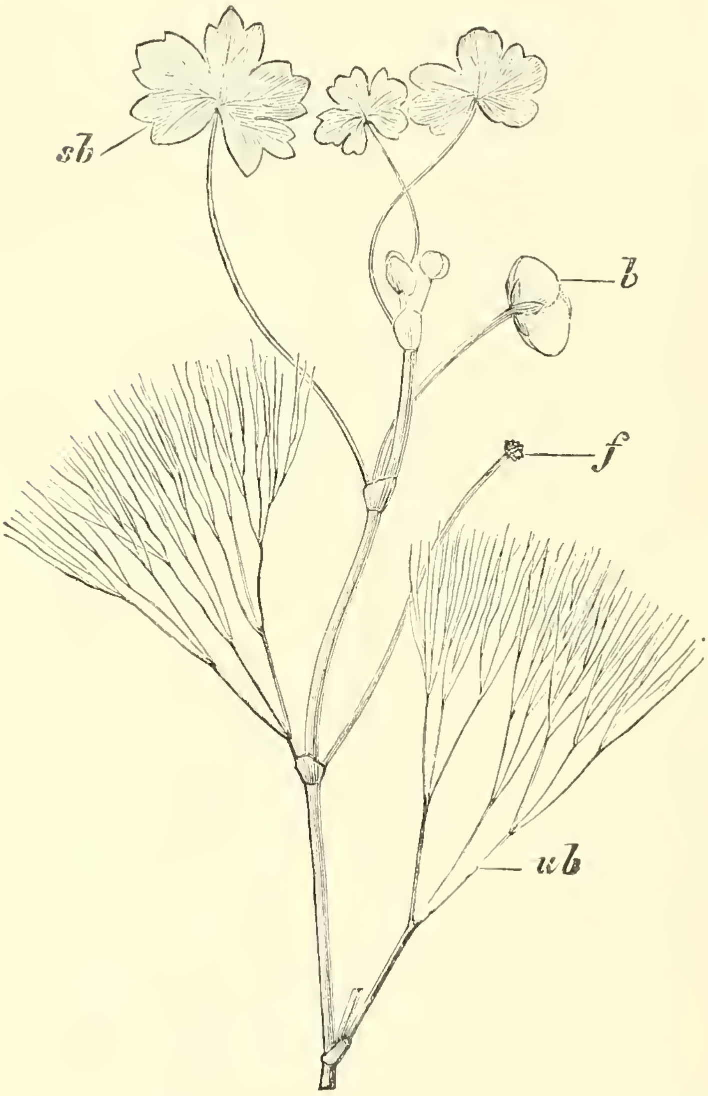


FIG. 34.—*Ranunculus aquatilis*. *ub*, Submerged leaves; *sb*, floating leaves; *b*, flower; *f*, fruit. (Reduced.)

Mimosa, their stalklets articulate with the spindle by means of swollen pulvini. The term PEDATE is applied to leaves on which segments are further divided on one side only, and the new segments are similarly divided (Fig. 37, *l*). Variations in the outline of leaves, whether they are entire, serrate, dentate, crenate, incised, etc., as well as peculiarities in their shape and segmentation, are of use in the determination of plants. The VENATION or NERVATURE of leaves is also taken into consideration, and leaves are in this respect described according to the direction of their so-called veins or nerves, as PARALLEL VEINED or NETTED VEINED. In parallel venation the veins or nerves run either approximately parallel with each other or in curves, converging at the base and apex of the leaf (Fig. 35, *s*); in netted veined leaves (Fig. 180) the veins branch off from one another, and gradually decrease in size until they form a fine anastomosing network. In leaves with parallel venation the parallel main nerves are usually united by weaker cross veins. Netted or reticulately veined leaves in which the side veins run from the median main nerve or MIDRIB are further distinguished as PINNATELY VEINED, or as PALMATELY VEINED when several equally strong ribs separate at the base of the leaf-blade, and give rise in turn to a network of weaker veins. Parallel venation is characteristic, in general, of the Monocotyledons; reticulate venation, of Dicotyledons. Monocotyledons have usually simple leaves, while the leaves of Dicotyledons are often compound, and are also more frequently provided with stalks.

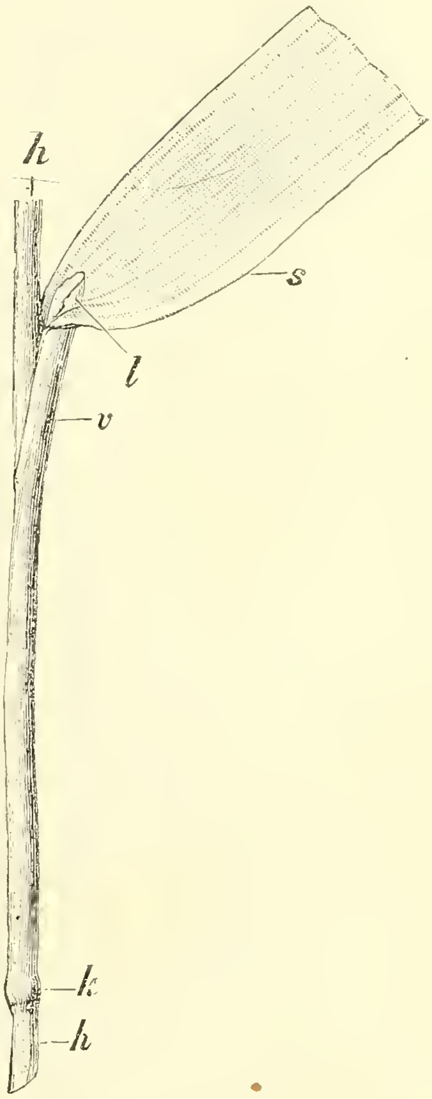


FIG. 35.—Part of stem and leaf of a grass. *h*, Haulm; *v*, leaf-sheath; *k*, swelling of the leaf-sheath above the node; *s*, part of leaf-blade; *l*, ligule. (Nat. size.)

The nerves or veins give to a leaf its necessary mechanical rigidity and render possible its flattened form. The branches of the veins parallel to the margin of most leaves prevent their tearing: when there are no such marginal nerves in large thin leaves, the lamina is easily torn into strips by the wind and rain. This frequently happens to the leaves of the Banana (*Musa*), which, consequently, when growing under natural conditions in the open air, presents quite a different appearance than when grown under glass. The leaves of the Banana, after becoming thus divided, offer less resistance to the wind. In a similar manner the leaves of Palms, although undivided in their bud state, become torn even during the process of their unfolding. A similar protection from injury is afforded to the Aroid (*Monstera*) by the holes with which its large leaf-blades become perforated. Equally advantageous results are secured by many plants whose leaves are, from their very inception, divided or dissected. The submerged leaves of aquatic plants, on the other hand, are generally finely divided or dissected, not only for mechanical purposes, but also to afford a more complete exposure of the leaf surface to the water. Accordingly, in such water-plants as *Ranunculus aquatilis* (Fig. 34), which possess both floating and submerged leaves, it is generally the latter only that are dissected and filiform in character. The pointed extremity of the foliage leaves of many land plants, according to STAHL, facilitates the removal of water from the leaf surface (drip-tips). According to RACIBORSKI, in several tropical climbing plants the development of the point of the leaf precedes that of the rest of the leaf, and for a time performs its functions. Fleshy so-called succulent leaves, like fleshy stems, serve as reservoirs for storing water.

Heterophylly.—Many plants are characterised by the development of different forms of foliage leaves. Such a condition is known as heterophylly. Thus the earlier leaves of *Eucalyptus globulus* are sessile and oval, while those subsequently formed are stalked and sickle-shaped. In other cases the heterophyllous character of the leaves may represent an adaptation to the surrounding environment, as in the Water Crowfoot (*Ranunculus aquatilis*), in which the floating leaves are lobed, while those entirely submerged are finely divided (Fig. 34).

The Leaf-base.—In Monocotyledons the leaf-base very often forms a SHEATH about the stem; in Dicotyledons this happens much less frequently. In the case of the *Gramineae*, the sheath is open on the side of the stem opposite the leaf-blade (Fig. 35, *v*), while in the *Cyperaceae* it is completely grown together. The sheath of the grasses is prolonged at the base of the lamina into a scaly outgrowth, the ligule. Such a sheath, while protecting the lower part of the internodes which remain soft and in a state of growth, gives them at the same time rigidity. STIPULES are lateral appendages sometimes found at the base of leaves. When present they may be either small and inconspicuous (Fig. 36, *nb*), or may attain a considerable size. When their function is merely to protect the young growth in the bud, they are usually of a brown or yellow colour, and are not persistent; whereas, if destined to become assimilatory organs, and to assist in providing nourishment, they are green, and may assume the structure and form of the leaf-blade, which sometimes becomes modified and adapted to other purposes (Figs. 48, 49). Normally, the stipules are two in number, that is, one on each side of the petiole. In many species of *Galium*, where the stipules resemble leaf-blades, the leaf-whorls appear to be composed of six members, but consist actually of but two leaves with their four stipules, which may be easily distinguished by the absence of any buds in their axils. In other species of the same genus (*Galium cruciatum* and *palustre*) there are only four members in the whorls, as each two adjoining stipules become united. In many cases, as in the Rose and the Clover, the stipules have the form of appendages to the enlarged leaf-base. Sometimes both stipules are united into a single one, which then appears to have an axillary origin; or the stipules may completely encircle the stem, and thus form a sheath about the younger undeveloped leaves. This sheath-like fusion of the stipules may be easily observed on the India-rubber tree (*Ficus elastica*), now so commonly grown as a decorative plant. In this case the stipular sheath is burst by the unfolding of each new leaf and pushed upwards on the stem. In the *Polygonaceae* the stipular covering is similarly torn apart by the developing leaves, but then remains on the stem in the form of a membranous sheath (ochrea).

Scale Leaves possess a simpler structure than foliage leaves, and are attached directly to the stem, without a leaf-stalk. They exercise no assimilatory functions, and are more especially of service as organs of protection. Scale leaves exercise their most important function as bud-scales (Fig. 36); they are then hard and thick, and usually of a brown colour. They most frequently take their origin from the enlarged leaf-base; in that case the upper leaf either does not develop, or exists only in a reduced condition at the apex of the scale. The true morphological value of scale leaves of this nature is very evident in the bud scales of the winter buds of the Horse-chestnut (*Aesculus Hippocastanum*); for, while the outer scales show no perceptible indications of an upper leaf, small leaf-blades can be distinctly distinguished at the apices of the inner scales. In other cases the scale leaves are modified stipules (Fig. 36), and are then also derived from the leaf-base; while, in other instances, they correspond to the enlarged, but still undifferentiated, primordial leaves. The

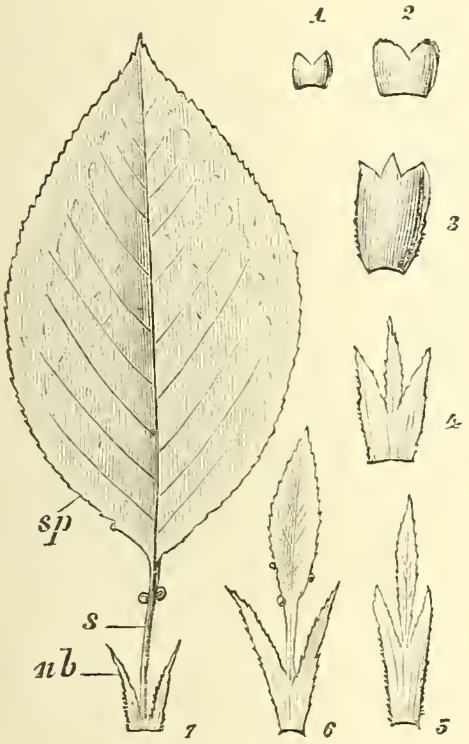


FIG. 36.—Bird Cherry (*Prunus Avium*). Bud-scales (1-3) and the transition form (4-6) to the foliage leaf (7). *sp*, Leaf-blade; *s*, leaf-stalk; *nb*, stipules. (Reduced slightly.)

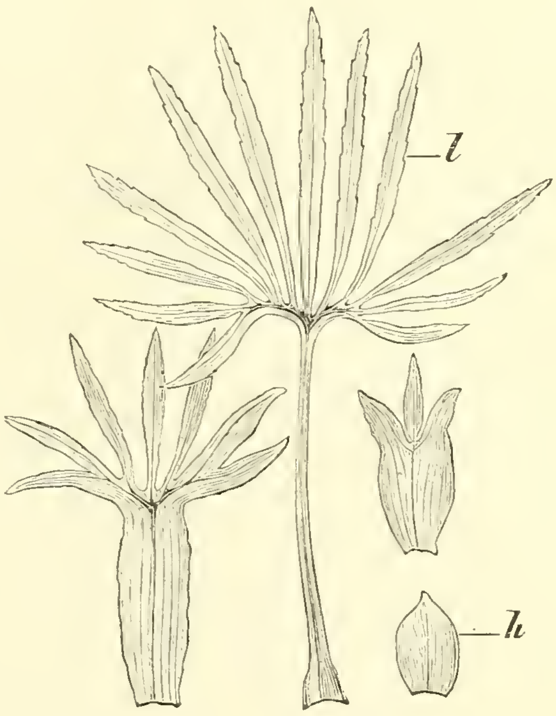


FIG. 37.—*Helleborus foetidus*. Foliage leaf (*l*) and intermediate forms between this and the bract (*h*). (Reduced.)

bud-scales of the Oak are the stipules of leaves in which the laminæ are only represented by minute scales. Scale leaves, usually colourless and in various stages of reduction, are found on rhizomes (Figs. 23, 33), bulbs (Fig. 25), and tubers (Fig. 26). On the aerial stems arising from such subterranean shoots the formation of similar scale leaves generally precedes the development of the foliage leaves, with which they are connected by a series of transitional forms.

Bracteal Leaves resemble scale leaves in form, and have a similar development (Fig. 33, *hb*). They act as subtending leaves for the floral shoots, and are termed BRACTS. They are connected with foliage leaves by intermediate forms (Fig. 37). Though they are not infrequently green they may be otherwise coloured, or even altogether colourless.

Floral Leaves.—The modified leaves which form the flowers of Phanerogams are termed floral leaves. In the highest development attained by a phanerogamic flower (Fig. 38), the successive floral leaves are distinguished as sepals (*k*), petals (*c*), stamens (*a*), and carpels (*g*). In most cases the sepals are green and of a firm structure; the petals, on the other hand, are more delicate and variously coloured. The stamens are generally filamentous, and produce the pollen in special receptacles. The carpels more closely resemble scale leaves, and by closing together form receptacles within which the ovules are produced. The stamens and carpels of Phanerogams correspond to the spore-bearing leaves of the Vascular Cryptogams. Such spore-bearing leaves are termed SPOROPHYLLS, and even in the Vascular Cryptogams exhibit a greater or less departure from the form of other foliage leaves.

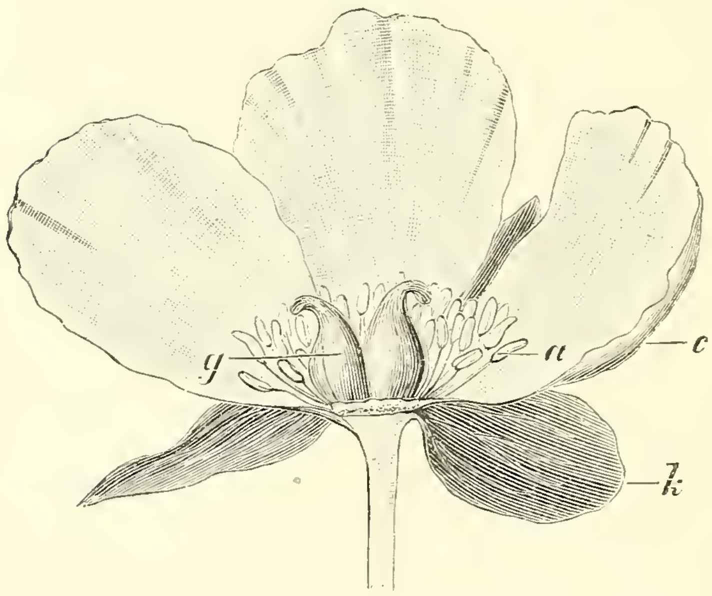


Fig. 38.—Flower of *Paeonia peregrina*. *k*, Sepals; *c*, petals; *a*, stamens; *g*, carpels. Part of the sepals, petals, and stamens have been removed to show the pistil, consisting of two separate carpels. (Half nat. size.)

It is evident that the scale and bracteal leaves are to be considered as rudimental foliage leaves, not only from the mode of their development but also from the possibility of transforming them into foliage leaves. GOEBEL, by removing the growing tip and foliage leaves of a shoot, succeeded in forcing it to develop other foliage leaves from its scale leaves (11). Rhizomes, grown in the light, develop foliage leaves in place of the usual scale leaves, and even on a potato it is possible to induce the formation of small foliage leaves instead of the customary scale leaves.

Leaf-Scars.—After a leaf has fallen, its previous point of insertion on the stem is marked by the cicatrix or scar left by the fallen leaf. In winter, accordingly, when the trees are denuded of their leaves, the axillary buds are plainly perceptible above the leaf-scars.

Vernation and Æstivation.—A section through a winter bud shows a wonderful adaptation of the rudimentary leaves to the narrow space in which they are confined (Fig. 39). They may be so disposed that the separate leaves are spread out flat, but more frequently they are folded, either cross-wise or length-wise on the midrib (conduplicate), or in longitudinal plaits, like a fan (plaited, plicate); or they may be crumpled with no definite arrangement of the folds; or each leaf may be rolled, either from the tip downwards (circinate) or longitudinally, from one margin to the other (convolute), or from both margins towards the midrib, either outwards (revolute) or inwards (involute, Fig. 39, *l*). The manner in which each separate leaf is disposed in the bud is termed VERNATION. On the other hand, the arrangement of the leaves in the bud with respect to one another is designated ÆSTIVATION. In this respect the leaves are distinguished as FREE when they do not touch, or VALVATE when merely touching, or IMBRICATED, in which case some of the leaves are overlapped by others (Fig. 39, *k*). If, as frequently occurs in flower-buds, the margins of the floral leaves successively overlap each other in one direction, obliquely or otherwise, the æstivation is said to be CONTORTED.

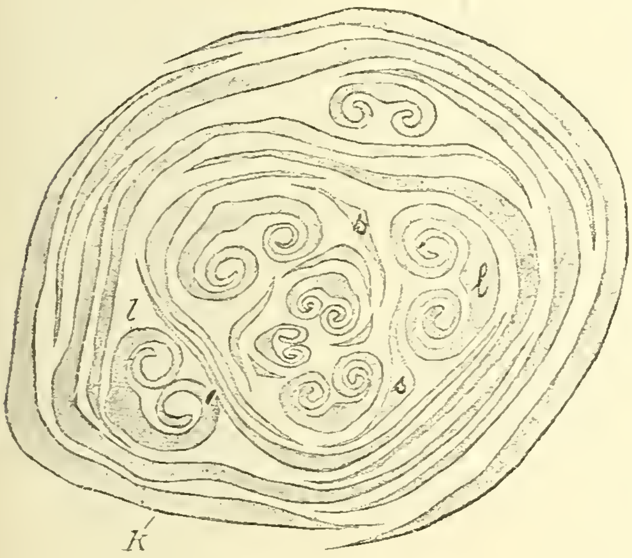


FIG. 39.—Transverse section of a bud of *Populus nigra*. *k*, Bud-scales showing imbricated æstivation; *l*, foliage leaves with involute vernation; *s*, each leaf has two stipules. (×15.)

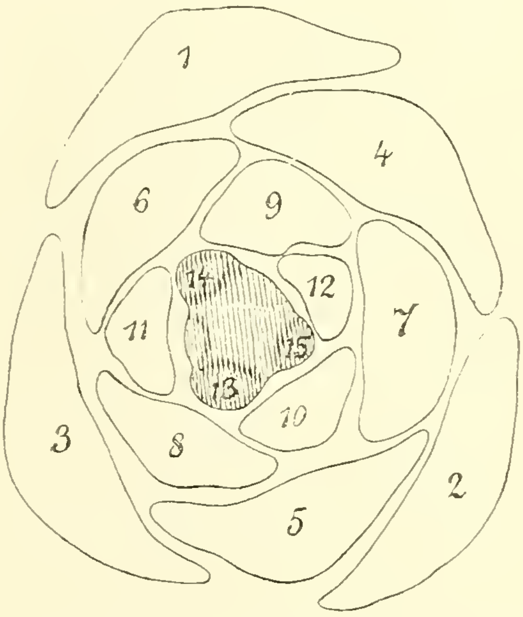


FIG. 40.—Transverse section of a leaf-bud of *Tsuga canadensis*, just below the apex of the shoot, showing a $\frac{5}{13}$ divergence. (After HOFMEISTER.)

The Arrangement of Leaves.—In all erect elongated shoots, and still more so in dwarf shoots, it is apparent that there is a marked regularity in the arrangement of leaves. This regularity may be most easily recognised in cross-sections of buds (Fig. 39), particularly in sections showing the apex of the vegetative cone (Fig. 31). From such an apical section it is easily seen that the regularity in the order of arrangement of the rudimentary leaves is determined by their conformity with the position of the older leaves on the vegetative cone, and the consequent necessity of utilising the remaining free space. Thus, the position of newly developing leaves is influenced by those already existing, while their formation is the result of internal causes. After the rudiments of the new leaves have become protruded from the vegetative cone, they come in direct contact with the older leaves, and may then, as SCHWENDENER (12) has shown, become displaced through the consequent mutual pressure, by which corresponding changes in their ultimate position may be effected. If the axis does not grow in length, but only in thickness, as the rudimentary leaves increase in size, their points of insertion will be displaced laterally by longitudinal pressure ; if the axis increases in length, and not in thickness, the insertion of the leaves will be displaced by a transverse pressure. The arrangement of the leaves would also be affected by any increase or decrease in the size of the vegetative cone, unaccompanied by a corresponding increase or cessation of the growth of the rudimentary leaves. Abrupt changes in the usual position of the leaves may also be occasioned by the torsion of their parent stem. Thus, the leaves of *Pandanus* first appear in three straight rows on the vegetative cone, and their subsequent spiral arrangement, according to SCHWENDENER, results from the torsion of the stem. An irregular arrangement of the leaves, such as occurs, for example, on the flower-stalk of the Crown Imperial (*Fritillaria imperialis*), may result from the unequal size of the leaves at the time of their inception on the vegetative cone. Some modes of leaf arrangement, on the other hand, are difficult to explain by the mutual contact and displacement of the leaf rudiments, and constitute objections to SCHWENDENER'S theory.

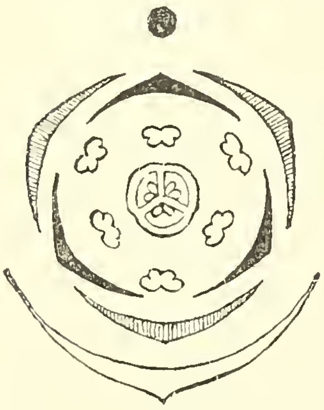


FIG. 41.—Diagram of a Liliaceous flower. The main axis is indicated by a black dot, opposite to which is the bract.

A frequent mode of arrangement of foliage leaves is the decussate, in which two-leaved whorls alternate with each other (Fig. 31). A whorled arrangement is characteristic of floral leaves. When the number of leaves in each whorl is the same the whorls usually alternate. On the other hand, the number of members in the different whorls of floral leaves will often be found to vary greatly ; or a whorl, the existence of which would be expected from the position of other whorls and from a comparison with allied plants, may be altogether wanting. In this connection a comparison of the flowers of the *Liliaceae* and *Iridaceae* will be instructive. The flowers of the *Liliaceae* (Fig. 41) are composed of five regularly alternating, three-leaved whorls or cycles, viz. a calyx and a corolla (each consisting of three leaves, and on account of their similar appearance usually referred to conjointly as the PERIANTH), an outer and an inner cycle of stamens, and finally, in the centre of the flower, an ovary of three carpels. In the flowers of the *Iridaceae* (Fig. 42) the arrangement is exactly similar, except that one whorl, that of the inner cycle of stamens, is lacking, but the three carpels are situated exactly as if the missing cycle of stamens were present. From this similarity of arrangement, despite the absence of the one cycle of stamens, the conclusion has been drawn that, at one time, the inner row of stamens was actually present, but has now disappeared. In constructing a THEORETICAL DIAGRAM of the *Iridaceae* the missing cycle of stamens is indicated by some special sign (by crosses in Fig. 42); a diagram in which theoretical suppositions are not taken into consideration is called an EMPIRICAL DIAGRAM. Diagrams showing the alternate arrangement of leaves, in cases where only a single leaf arises from each node, may be constructed by projecting the successive nodes of a stem upon a plane

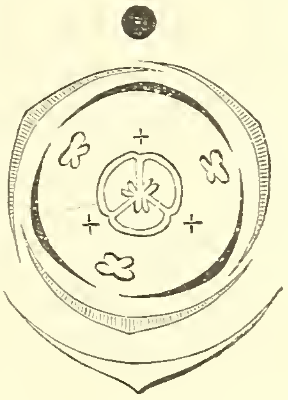


FIG. 42.—Theoretical diagram of the flower of the Iris. The absent cycle of stamens is indicated by crosses.

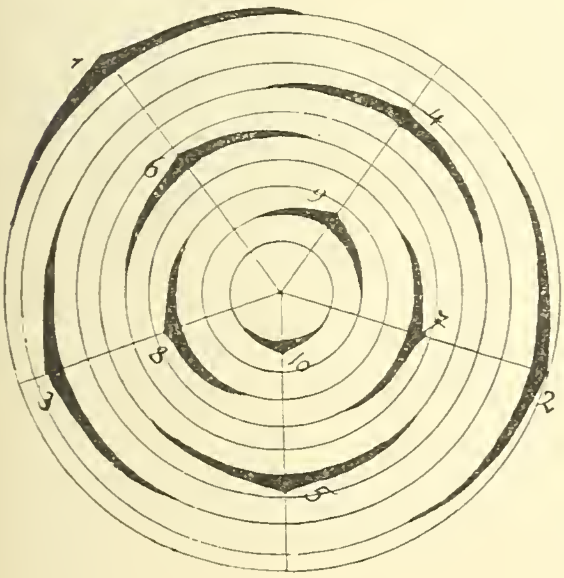


FIG. 43.—Diagram showing $\frac{2}{5}$ position of leaves. The leaves numbered according to their genetic sequence.

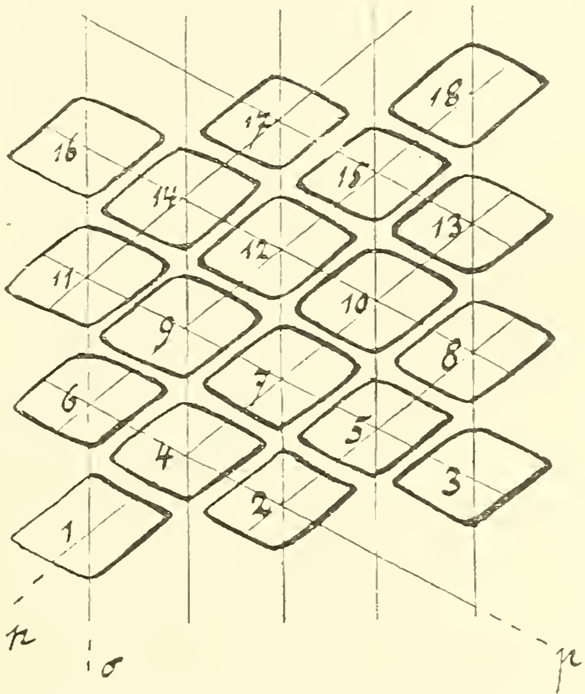


FIG. 44.—The $\frac{2}{5}$ position on the outspread surface of the axis. *o*, Orthostichies; *p*, parastichies. The leaves are numbered according to their genetic sequence.

by means of a series of concentric circles, on which the position of the leaves may be indicated (Fig. 43). The angle made by the intersection of the median planes of any two successive leaves is called their DIVERGENCE, and is expressed in fractions of the circumference; for example, in case the angular divergence between two successive leaves is 120°, their divergence is expressed by the fraction $\frac{1}{3}$. In the adjoining diagram (Fig. 43) a $\frac{2}{5}$ divergence is indicated. Where the lateral distance between two successive leaves is $\frac{2}{5}$ of the circumference of the stem, the sixth leaf is above the first, the seventh above the second, and so on. The leaves form on the axis five vertical rows, which are spoken of as ORTHOSTICHIES. Where the leaves are very much crowded, as in dwarf-shoots, a set of spiral rows called PARASTICHIES, due to the contact of the nearest laterally adjacent members, becomes much more noticeable than the orthostichies. If the surface of such an axis be regarded as spread out horizontally, the parastichies become at once distinguishable (Fig. 44), and it will be evident that the sum of the parastichies cut by every cross-section through such an axis must equal the number of the orthostichies. On objects like pine cones, in which the parastichies are easily recognised, they may be used to determine the leaf arrangement. The most common divergences are the following, $\frac{1}{2}$, $\frac{1}{3}$, $\frac{2}{5}$, $\frac{3}{8}$, $\frac{5}{13}$, $\frac{8}{21}$, $\frac{13}{34}$, etc. In this series it will be observed that in each fraction the numerator and denominator are the sum of those of the two preceding fractions. The value of the different fractions varies, accordingly, between $\frac{1}{2}$ and $\frac{1}{3}$, while always approaching a divergence angle of $137^\circ\ 30'\ 28''$. The frequent recurrence of the divergence angles, expressed by the fractions of this series, is, no doubt, due to the fact that by such arrangements of the leaves, the space available is utilised to the best advantage, and with the least possibility of mutual hindrance in the performance of the assimilatory functions. If a line be drawn on the surface of a stem, so as to pass in the shortest way successively through the points of insertion of every leaf, a spiral called the GENETIC SPIRAL will be constructed. That portion of the genetic spiral between any two leaves directly over each other on the same orthostichy is termed a CYCLE. Where the divergence is $\frac{2}{5}$, a cycle will accordingly include five leaves, and will in such a case have made two turns about the stem. An attempt has been made to trace spirals even where the leaves are arranged in whorls, but such a procedure seems rather superfluous. It is, moreover, no longer attempted to extend the spiral theory to dorsiventral shoots; since it is now known that this arrangement of the leaves is due, not to an ideal spiral law, but to mechanical causes regulating their development. The tips of dorsiventral shoots are frequently coiled ventrally inwards, bearing their leaves either dorsally or on the sides, but, in the latter case, more on the dorsal than ventral surface. The creeping stems of many Ferns or the flower-bearing shoots of Forget-me-not (*Myosotis*) are good examples of such dorsiventral shoots. The line joining successive leaves in such cases is, at the best, but a zigzag.

The Metamorphosis of Foliage Leaves.—A form of slightly modified foliage leaves is seen in peltate leaves, or those of which the petioles are attached to their lower surfaces somewhat within the margin, as in the leaves of the Indian Cress (*Tropaeolum majus*, Fig.

181). In the process of their development the young leaf-blades, in this case, grow not only in the same direction as the petioles, as a prolongation of them, but also horizontally in front of them. The tabular leaves of many insectivorous plants may have commenced their development in much the same way. The leaves of *Nepenthes robusta* (Fig. 45), for example, in the course of adaptation to the performance of their special function, have acquired the form of a pitcher with a lid which is closed in young leaves, but eventually opens. The pitcher, as GOEBEL has shown, arises as a modification of the leaf-blade. At the same time the leaf-base becomes expanded into a leaf-like body, while the petiole between the two parts sometimes fulfils the office of a tendril. By a similar metamorphosis of its leaflets, bladder-like cavities are developed on the submerged leaves of *Utricularia* (Fig. 46). The entrance to each bladder is fitted with a small valve which permits the ingress but not the egress of small water-animals. While such leaves display a progressive metamorphosis, in other instances the modifications are of the nature of a reduction. A metamorphosis of the whole leaf lamina, or a part of it, into tendrils (LEAF-TENDRILS) is a comparatively frequent occurrence, especially among the *Papilionaceae*. In the adjoining figure of a Pea leaf (Fig. 47), the upper pair of leaflets have become transformed into delicate tendrils which have the power of twining about a support. In the case of the yellow Vetchling, *Lathyrus Aphaca* (Fig. 48), the whole leaf is reduced to a tendril and the function of leaf-blade is assumed by the stipules (n). A comparison between these two forms is phylogenetically instructive, as it indicates the steps of the gradually modifying processes which have resulted in the complete reduction of the leaf lamina of *Lathyrus*. The

FIG. 45.—*Nepenthes robusta*. ($\frac{1}{5}$ nat. size.)

comparison of the two preceding cases with *Ampelopsis* (Fig. 29) will make the distinction between leaf-tendrils and stem-tendrils clear, and indicate the value of comparative morphological investigation.

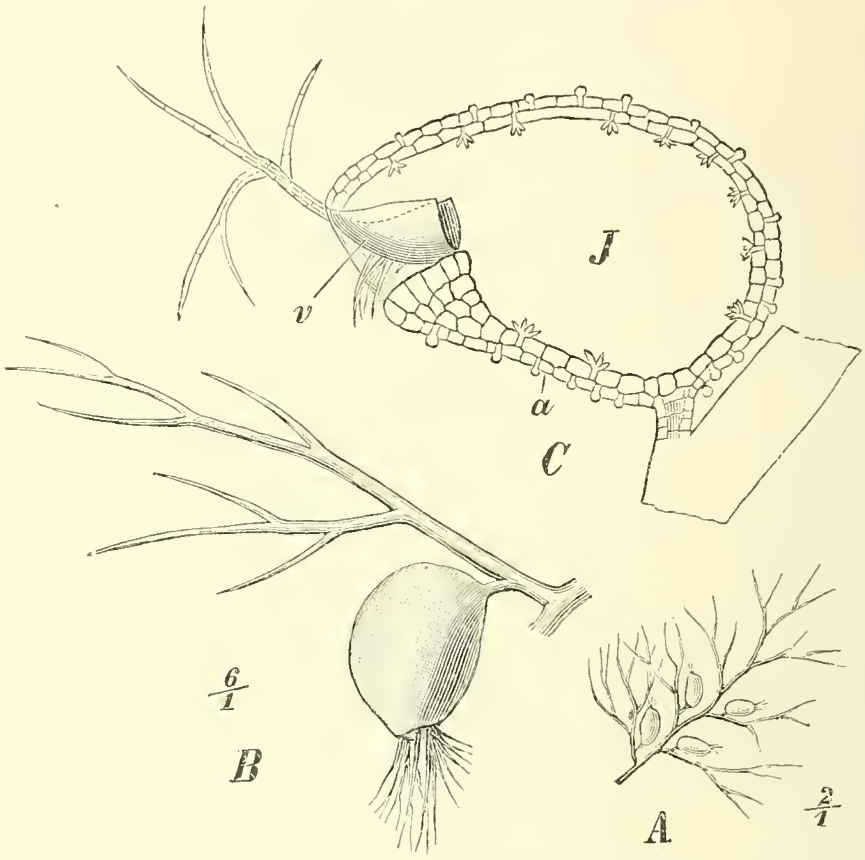


FIG. 46.—*Utricularia vulgaris.* *A*, Part of leaf with several bladders (×2). *B*, Single pinnule of leaf with bladder (×6). *C*, (after GOEBEL), Longitudinal section of a bladder (×28); *v*, valve; *a*, wall of bladder; *J*, cavity of bladder.

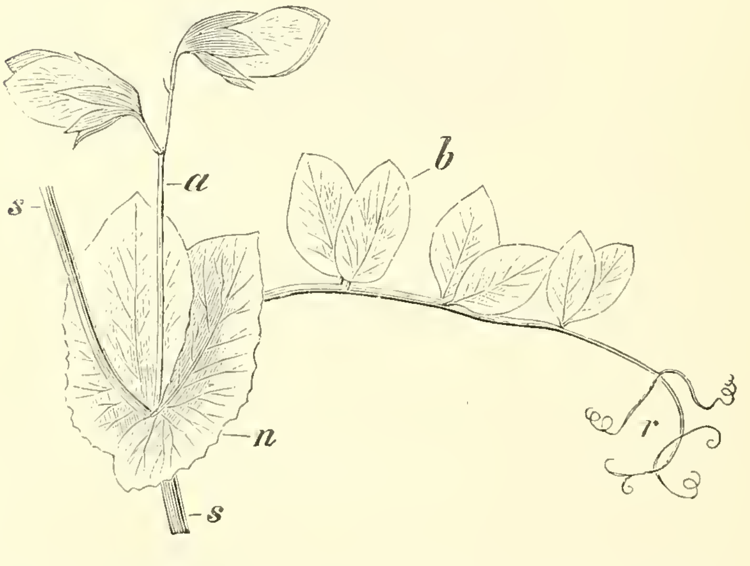


FIG. 47.—Portion of stem and leaf of the common Pea, *Pisum sativum.* *s*, Stem; *n*, stipules; *b*, leaflets of the compound leaf; *r*, leaflets modified as tendrils; *a*, floral shoot. (½ nat. size.)

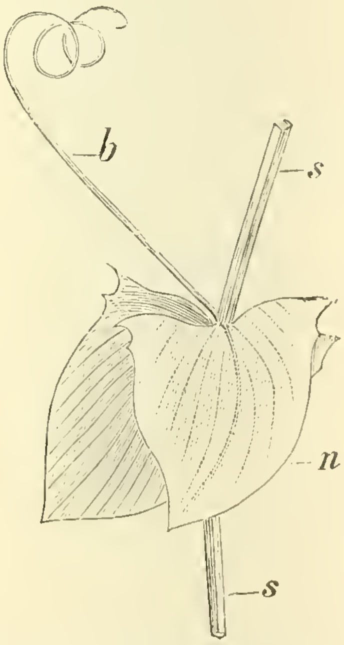


FIG. 48.—*Lathyrus Aphaca.* *s*, Stem; *n*, stipules; *b*, leaf-tendril. (½ nat. size.)

In *Lathyrus Aphaca* the stipules assume the function of the metamorphosed leaf laminæ; in other instances, as in the case of the

Australian Acacias (Fig. 54, 7, 8, 9), it is the leaf petioles which, becoming flattened and leaf-like in appearance, supply the place of the undeveloped leaf-blades. Such a metamorphosed petiole is called a PHYLLODE, and, except that it is expanded perpendicularly, exactly resembles a cladode. From the latter, however, it is morphologically different, for the one represents a metamorphosed petiole, the other a metamorphosed shoot. In accordance with this distinction phyllodes do not, like cladodes, spring from the axils of leaves. Just as stems become modified into thorns (Fig. 30), by a similar metamorphosis leaves may be converted into leaf thorns. Whole leaves on the main axis of the Barberry (*Berberis vulgaris*) become thus transformed into thorns, usually three, but in their character of leaves still give rise to axillary shoots provided with foliage leaves. By a similar metamorphosis, the two stipules of the leaves of the common Locust (*Robinia Pseudacacia*) become modified into thorns, while the leaf lamina persists as a foliage leaf (Fig. 49).

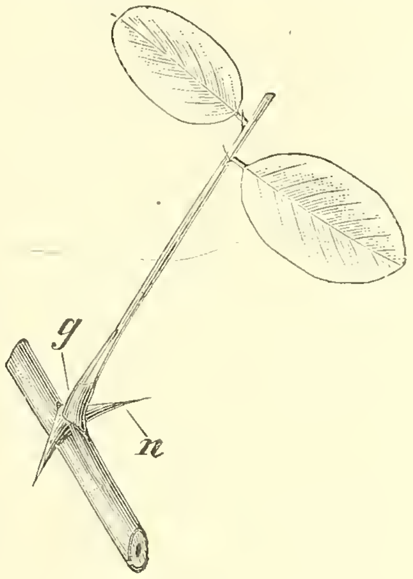


FIG. 49.—Part of stem and compound leaf of *Robinia Pseudacacia*. *n*, Stipules modified into thorns; *g*, leaf-cushion. (½ nat. size.)

The Root

The third member of the plant body of Cormophytes, in its typical development as an UNDERGROUND ROOT, shows but little variation. This regularity of form is due to the uniformity of the conditions to which roots are exposed in the ground, for AERIAL ROOTS, which are for the most part restricted to the moist climate of the tropics, exhibit a much greater tendency to modification. The covered vegetative cone and the inability to develop leaves are characteristic of roots, and furnish an easy means of distinguishing them from underground shoots. A ROOT-CAP or CALYPTRA affords the vegetative cone of a root the protection that is provided to the apex of a stem by the rudimentary leaves. Although, generally, the existence of a root-cap is only disclosed by a median, longitudinal section through the root-tip, in some roots it is plainly distinguishable as a cap-like covering. The very noticeable caps on the water roots of Duckweed (*Lemna*) are not, in reality, root-caps, as they are not derived from the root, but from a sheath which envelops the rudimentary root at the time of its origin. They are accordingly termed ROOT-POCKETS. As a general rule, however, roots without root-caps are of rare occurrence, and in the case of the Duckweed the root-pockets perform all the functions of a root-cap. The short-lived roots of the Dodder (p. 26) afford another example of roots devoid of root-caps. Characteristic of roots are also the ROOT-HAIRS (Fig. 53, *r*), which are found at a short distance from their apices. As the older root-hairs die at the same rate that the new ones are developed, only a small portion of a root is provided with root-hairs at the same time. In some few instances roots develop no root-hairs; this is true of the roots of many Conifers, and of most aerial roots.

Branching of the Root.—Just as the shoot may become bifurcated by the division of its growing point (Fig. 18), so a root may become similarly branched. For the most part, this mode of branching takes place only in the roots of *Lycopodiaceae*, the shoots of which are also dichotomously branched (p. 19). The branching of roots usually occurs in acropetal succession, but the lateral roots (Fig. 53, *sw*) make their appearance at a much greater distance from the growing point of the main root, than lateral shoots from the apex of their parent stem. By reason of the internal structure of their parent root, lateral roots always develop in longitudinal rows (Fig. 53). They are of endogenous origin, and before reaching the surface must break through the surrounding and overlying tissue of the parent root, by the ruptured portions of which they are often invested, as with a collar.

ADVENTITIOUS ROOTS, just as adventitious shoots, may arise from any part of a plant. They are especially numerous on the underside of rhizomes (Fig. 23, *w*), and also, when the external conditions are at all favourable, they seem to develop very readily from the stem nodes. A young shoot, or a cutting planted in moist soil, quickly forms adventitious roots, and roots may also arise in a similar manner from leaves, especially from *Begonia* leaves. The origin of adventitious roots, as of all roots, is endogenous. Dormant root rudiments occur in the same manner as dormant buds of shoots. The ease with which willows are propagated from shoots is well known, and is due to the promptness with which they develop adventitious roots from apparently latent embryonic tissue, when the requisite conditions of moisture and darkness are fulfilled.

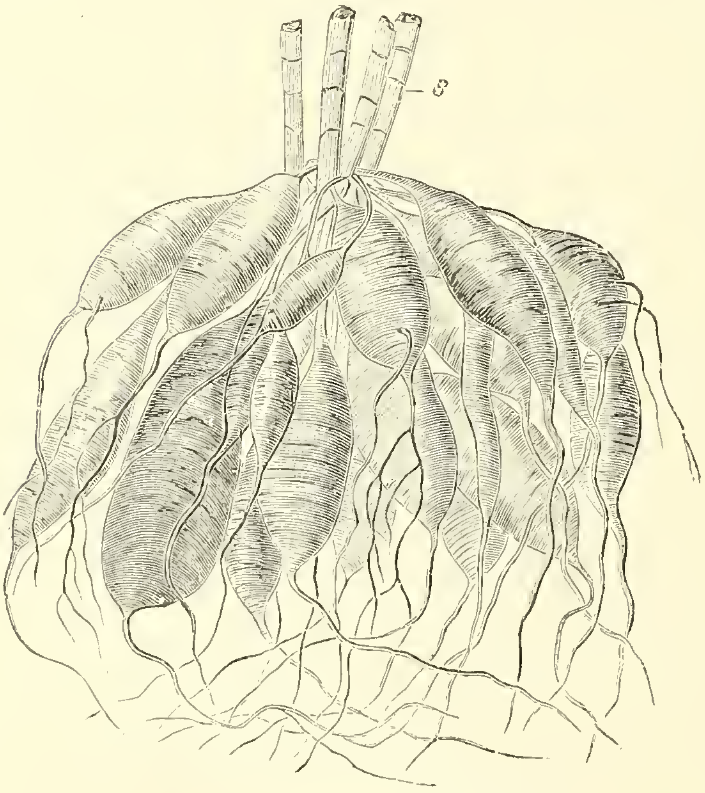


FIG. 50.—Root-tubers of *Dahlia variabilis*. *s*, The lower portions of cut stems. (¼ nat. size.)

The Metamorphosis of the Root.—The customary nomenclature for the various root forms is based on their shape, size, and mode of branching. A root which is a prolongation downwards of the main stem is called the main root or TAP-ROOT; the other roots are termed, with reference to the tap-root, LATERAL ROOTS of different orders, according to the order of their development. A tap-root is present in Gymnosperms and many Dicotyledons, while it is, as a rule, wanting in Monocotyledons. The root system of most Monocotyledons and many Dicotyledons mainly consists of adventitious roots arising from the base of the stem. The roots may enlarge and become turnip-shaped or tuberous (Fig. 50). Such tuberous growths often greatly resemble stem tubers, but may be distinguished from them by their root-caps, by the absence of any indications of leaf development, and by their internal structure.

The tubers of the *Orchidaceae* exhibit, morphologically, a peculiar mode of formation. They are, to a great extent, made up of fleshy, swollen roots, fused together and terminating above in a shoot-bud. At their lower extremity the tubers are either simple or palmately segmented. In the adjoining figure (Fig. 51) both an old (*t′*) and a young tuber (*t″*) are represented still united together. The older tuber has produced its flowering shoot (*b*), and has begun to shrivel and dry up; a bud, formed at the base of the shoot, in the axil of a scale leaf (*s*), has already developed the adventitious roots, which, swollen and fused together, have given rise to the younger tuber.

The **aerial roots** of tropical Epiphytes (13) differ considerably in their structure from underground roots. The aerial roots of the *Orchidaceae* and of many *Aroideae* are provided with a spongy sheath, the VELAMEN, by means of which they are enabled to absorb moisture from the atmosphere. Aerial roots, in some cases, grow straight downwards, and upon reaching the ground, branch and function as nutritive roots for the absorption of nourishment; in other instances, they turn from the light, and, remaining comparatively short and unbranched, fasten themselves as CLIMBING ROOTS to any support with which they come in contact. The climbing roots of many Orchids, Aroids, and Ferns branch and form lodgment places for humus; and into this the nutritive root branches penetrate as special outgrowths of the climbing roots. Pendent aerial roots generally contain chlorophyll. In the Orchid *Angraecum globulosum* the task of nourishing the plant is left entirely to the aerial roots, which are then devoid of a velamen, and very much flattened. They are distinctly green-coloured, and supply the place of the leaves which lose their green colour and are reduced to scales. The flat, dorsiventral, chlorophyll-containing roots of the tropical *Podostemaceae* (14) fulfil a similar

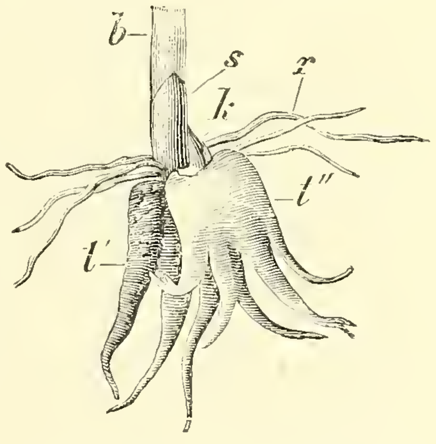


FIG. 51.—*Orchis latifolia.* *t′*, The old root-tuber; *t″*, the young root-tuber; *b*, floral shoot; *s*, scale leaf with axillary bud, *k*, from which the new tuber has arisen; *r*, ordinary adventitious roots. (½ nat. size.)

function. The aerial roots of the epiphytic *Bromeliaceae* are developed exclusively as climbing roots, while the leaves function not only as assimilating organs, but also assume the whole task of water-absorption. All the aerial roots of Epiphytes are, so far as their origin is concerned, adventitious.

The numerous adventitious roots which form a thickly-matted covering on the trunks of Tree-ferns become hard after death, and serve as organs of protection. In some Palms (*Acanthorrhiza, Iriartea*) the adventitious roots on the lower part of the stem become modified into thorns, ROOT-THORNS. The roots of certain tropical plants, such as *Pandanus* and the swamp-inhabiting Mangrove trees, are specially modified. These plants develop on their stems adventitious roots, which grow obliquely downwards into the ground, so that the stems finally appear as if growing on stilts. The Banyan trees of India (*Ficus Indica*) produce wonderful root-supports from the under side of their branches, upon which they rest as upon columns. The lateral roots of certain Mangrove trees become modified as peculiar breathing organs, and for this purpose grow upwards into the air out of the swampy soil or water in which the trees grow; they then become greatly swollen or flattened, and provided with special aerating passages. Such RESPIRATORY or AERATING ROOTS surround the Mangrove trees like vigorous Asparagus stalks, and enable the roots growing below in the mud to carry on the necessary exchange of gases with the atmosphere.

Reduction of Roots.—There is a general relation between the degree of development of the leaf-surface and of the root-system. In saprophytic and parasitic plants, the shoots of which are as a rule extremely reduced, a corresponding reduction of the root-system can be recognised. The roots of the Dodder (*Cuscuta*) form wart-like excrescences (Fig. 186, *H*) at the point of contact with their nourishing host, which they finally penetrate. They draw nourishment from the host plant, and are consequently termed SUCTION ROOTS or HAUSTORIA; such haustoria divide within their host into single filaments, and from each filament a new parasitic plant may be formed. The immense flowers of *Rafflesia Arnoldi*, which spring directly from the roots of *Cissus*, owe their origin to similar haustoria. The reduction of the roots may extend to such a degree that, in many plants, no roots are formed. It has been already mentioned that in the case of *Coralliorrhiza innata* (Fig. 24) the rhizome assumes all the functions of the roots, which are entirely absent. Also in many aquatics, *Salvinia, Wolffia arrhiza, Utricularia, Ceratophyllum*, roots are altogether absent.

Emergences.—The outgrowths from the surface of the plant body included under the term emergence must not on that account be regarded as homologous. A phylogenetic significance cannot be attached to the term as here used. It includes structures of the most different origin belonging both to the thallus and the cormus. The rhizoids, which serve to fasten the thallus of many Thallophytes and the cormus of the cormophytic *Bryophyta* to the substratum, as well as the massive attaching organs of many Brown Sea-weeds (*Fucaceae* and *Laminariaceae*) are classed here. So also are the structures which contain the asexual and sexual reproductive cells of the cryptogams (sporangia and sexual organs.) In the sense of the term implied here the hairs, prickles, and glands borne on the surface of the highly organised plants must be included. As an extreme case the attaching organs (hapteræ) of the previously mentioned *Podostemaceae* may be referred to. These hapteræ serve to attach the vegetative body of these plants firmly to the rocks exposed to rapidly flowing water, upon which they grow. They are at first conical outgrowths, but flatten out and become lobed when applied to the surface of the rock. This example is instructive since it shows that even in phanerogamic plants structures of considerable size and definite form may arise which cannot be regarded as modified roots or shoots. There is, indeed, no reason why outgrowths of the vegetative body of the plant should not become adapted to the performance of particular functions (15).

The Ontogeny of Plants

Just as in the phylogenetic development of the vegetable kingdom there is an evolution from simpler to more complex forms, so each plant in its ontogeny passes through a similar process of evolution. The study of the ontogenetic development of a plant is termed EMBRYOLOGY. A young plant, in its rudimentary, still unformed condition, is called an EMBRYO or GERM; and the early stages of its development are spoken of as GERMINATION. As a rule, the embryo, in the beginning of its development, is microscopic and of a spherical form. In a lower organism this condition may continue from the beginning to the end of its development, as is the case in *Gloeocapsa polydermatica* (Fig. 1, p. 11); or the development may proceed further to the formation of filamentous, ribbon-like or cylindrical bodies. If the future plant is to have a growing point, a part of the germ substance is retained in its embryonic condition, and further development proceeds from this embryonic substance. In the more highly-organised plants the different members arising from the growing point only gradually attain that degree of development characteristic of the particular plant. The plant must develop and attain maturity, and it is not until it has accomplished this that certain portions of the embryonic substance of the growing point are appropriated to the production of new embryos.

The different generations arising from an embryo of a plant may exactly resemble each other, or an ALTERNATION OF GENERATIONS may occur, in which case each succeeding generation is unlike its immediate predecessor. As a general rule, the alternate generations are equivalent, although this is not necessarily the case. One of the alternating generations is usually sexually differentiated, that is, its reproductive cells are only capable of development after a fusion with other reproductive cells. This process of the fusion of two sexually differentiated cells is called FERTILISATION, and its product a fertilised egg. The asexual generation, on the contrary, produces reproductive cells, termed SPORES, which require no fertilisation before germinating. In the case of the Thallophytes, the alternation of generations is often extremely complicated by the irregularity of the recurrence of the different generations, and by the interposition of other modes of reproduction, not in line with the regular succession of generations. In the Cormophytes, however, asexual and sexual generations regularly alternate, and consequently, whenever an alternation of generation occurs, more than one generation is requisite to complete a cycle in the development of a species. Accordingly, in the conception of a species, two or more individuals are included. These individuals may exist separately and distinct from each other, or they may be so united as to appear but a single organism; as, for example, in the

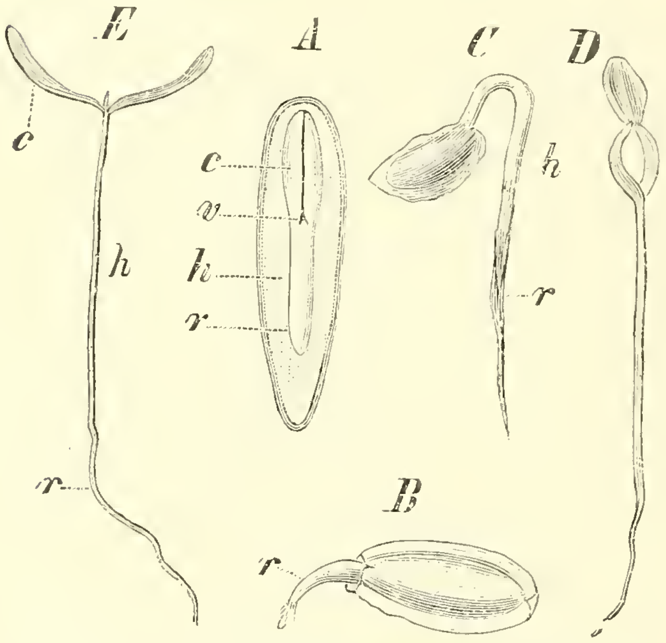


FIG. 52.—*Thuja occidentalis*. *A*, Median longitudinal section through the ripe seed (×5); *B*, *C* (×2); *D*, *E* (nat. size), different stages of germination; *h*, hypocotyl; *c*, cotyledons; *r*, radicle; *v*, vegetative cone of stem.

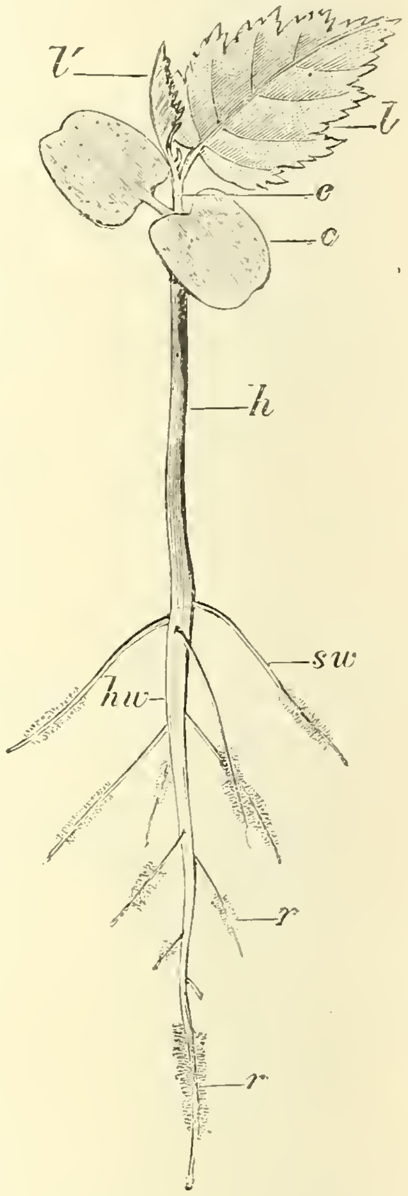


FIG. 53.—Seedling of *Carpinus Betulus*. *h*, hypocotyl; *c*, cotyledons; *hw*, main root; *sw*, lateral roots; *r*, root-hairs; *e*, epicotyl; *l*, *l'*, foliage leaves. (Nat. size).

Mosses, where the spore-producing generation lives upon the sexual plant, or as in Phanerogams, where, conversely, the sexual generation completes its development within the asexual plant.

In Phanerogams, owing to the formation of the embryo within seeds, that stage of the development of a plant which is termed germination is clearly defined; for not until the seed is completely formed does the newly-formed plantlet begin its independent existence. The embryo, while still enclosed within the seed, generally exhibits the segmentations characteristic of Cormophytes. Protected by the hard seed-coats, it is enabled to sustain a long period of rest. Abundant deposits of nutritive material in the embryo itself, or surrounding it, are provided for its nourishment during germination. The different segments of a phanerogamic embryo have received distinctive names; thus, as in the embryo of the American Arbor Vitae (*Thuja occidentalis*, Fig. 52), the stem portion (*h*) is termed the HYPOCOTYL, the first leaves (*c*) are the SEED LEAVES or COTYLEDONS, while the root (*r*) is distinguished as the RADICLE. The tap-root of the fully-developed plant is formed by the prolongation of the radicle. In Fig. 53 a germinating plantlet of the Hornbeam (*Carpinus Betulus*) is shown with its hypocotyl (*h*) and both cotyledons (*c*); but its radicle has already developed into a tap-root (*hw*) with a number of lateral roots (*sw*). An internode and foliage leaf (*l*) have been produced from the vegetative cone of the stem; while the next higher internode is also distinguishable, but has not yet elongated, and a second foliage leaf (*l′*) is unfolding.

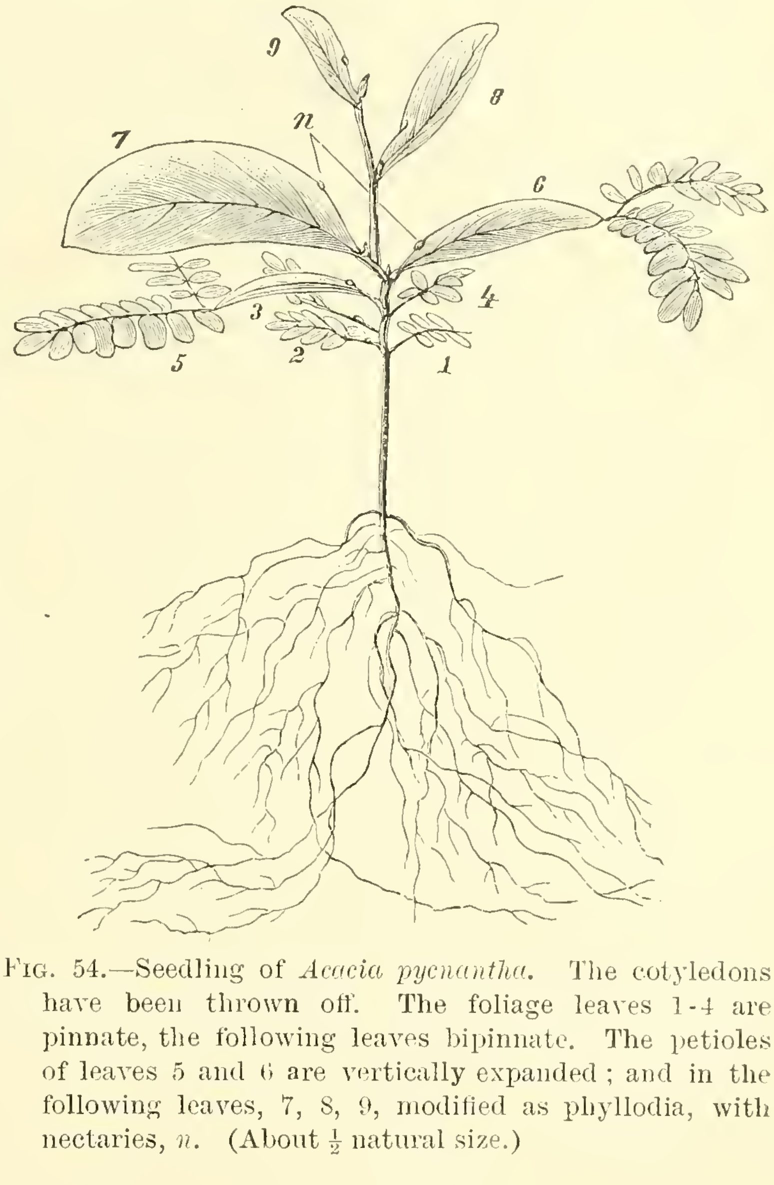


FIG. 54.—Seedling of *Acacia pycnantha*. The cotyledons have been thrown off. The foliage leaves 1-4 are pinnate, the following leaves bipinnate. The petioles of leaves 5 and 6 are vertically expanded; and in the following leaves, 7, 8, 9, modified as phyllodia, with nectaries, *n*. (About ½ natural size.)

A highly organised plant, which begins its development with the simplest stages and gradually advances to a higher state of differentiation, repeats in its ontogeny its phylogenetic development. In the process of its ontogenetic development much has been altered, and much omitted, so that it presents but an imperfect picture of its past history; nevertheless, this representation is valuable, and, next to comparative methods, furnishes the most important source of morphological knowledge. Whatever is true of the development of a plant from the embryo is also, as a rule, applicable to its further growth from the growing point, and, consequently, a knowledge of the mode of development at the growing point is of great importance in detecting homologies. The earlier a characteristic makes itself apparent in the embryo, or the nearer it is to the growing point of the old plant, so much the greater is its value in determining the general relationships existing between the different plants; the later it is exhibited in the embryo, or the farther removed it is from the growing point of the plant, the less its general value, but the greater, in proportion, its importance in defining the character of a genus or species. From the fossil remains of former geological periods, it is safe to conclude that such Conifers as *Thuja*, *Biota*, and the various Junipers, that now have scale-like compressed leaves, have been derived from Conifers with needle-shaped leaves. This conclusion is further confirmed by the fact, that on the young plants of the scaly-leaved Conifers typical needle-shaped leaves are at first developed. The modified leaf forms do not make their appearance until the young plant has attained a certain age, while in some Junipers needle-shaped leaves are retained throughout their whole existence (16). Even still more instructive are the Australian Acacias, whose leaf-stalks become modified, as phyllodia (p. 43), to perform the functions of the reduced leaf-blades. The proof for such an assertion is furnished by a germinating plantlet of *Acacia pycnantha* (Fig. 54), in which the first leaves are simply pinnate, and the succeeding leaves bipinnate. In the next leaves, although still compound, the leaf-blades are noticeably reduced, while the leaf-stalks have become somewhat expanded in a perpendicular direction. At length, leaves are produced which possess only broad, flattened leaf-stalks. As many other species of this genus are provided only with bipinnate leaves, it is permissible on such phylogenetic grounds to conclude that the Australian Acacias have lost their leaf-blades in comparatively recent times, and have, in their stead, developed the much more resistant phyllodes as being better adapted to withstand the Australian climate. The appearance, accordingly, of the phyllodes at so late a stage in the ontogenetic development of these Acacias is in conformity with their recent origin. It may, in like manner, be shown that in the case of plants with similarly modified leaf forms, the metamorphosis of the leaves does not take place until after the cotyledons and the first foliage leaves have been developed, and it is then usually effected by degrees.

II. INTERNAL MORPHOLOGY

(Histology and Anatomy)

A. The Cell

1. Structure of the Cell

All plants, as all animals, are composed of elementary organs called cells. In contrast to animal cells, typical vegetable cells are surrounded by firm walls, and are thus sharply marked off from one another. In fact, it was due to the investigation of the cell walls that the cell was first recognised in plants. An English micrographer, Robert Hooke, was the first to notice vegetable cells. He gave them this name in his *Micrographia* in the year 1667, because of their resemblance to the cells of a honeycomb, and published an illustration of a piece of bottle-cork having the appearance shown in the adjoining figure (Fig. 55). Robert Hooke, however, was only desirous of exhibiting by means of different objects the capabilities of his microscope; consequently, the Italian, Marcello Malpighi, and the Englishman, Nehemiah Grew, whose works appeared almost simultaneously a few years after Hooke's *Micrographia*, have been regarded as the founders of vegetable Histology. The living contents of the cell, the real body or substance, was not recognised in its full significance until the middle of last century. Only then was attention turned more earnestly to this study, which has since been so especially advanced by Meyen, Schleiden, Hugo v. Mohl, Nägeli, Ferdinand Cohn, Pringsheim, and Max Schultze.

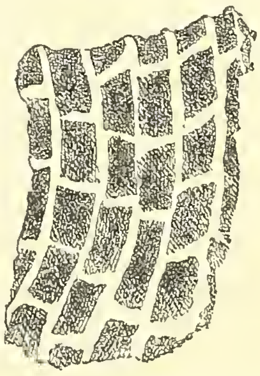


Fig. 55.—Copy of a part of Hooke's illustration of bottle-cork, which he entitled Schematism or texture of cork.

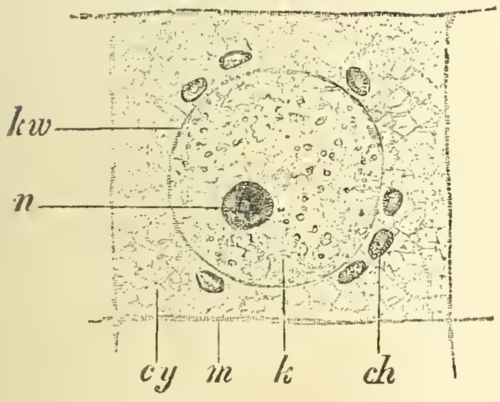


Fig. 56.—Embryonic cell from the vegetative cone of a phanerogamic plant. *k*, Nucleus; *kw*, nuclear membrane; *n*, nucleolus; *cy*, cytoplasm; *ch*, chromatophores; *m*, cell wall. (Somewhat diagrammatic, × circa 1000.)

If an examination be made of a thin longitudinal section of the apex of a stem of a phanerogamic plant, with a higher magnifying power than that used in the previous investigation (Fig. 17) of the vegetative cone, it will be seen that it consists of nearly rectangular cells (Fig. 56), which are full of protoplasm and separated from one another by delicate walls. In each of the cells there will be clearly distinguishable a round body (*k*), which fills up the greater part of the cell cavity. This body is the cell NUCLEUS. If sections, made in different directions through the vegetative cone, be compared with one another, it will be seen that its component cells are nearly cubical or tabular, while the nuclei are more or less spherical or disc-shaped. The finely granular substance (*cy*) filling in the space between the nucleus (*k*) and the cell wall (*m*) is the CELL PLASM or CYTOPLASM. In the cytoplasm there are to be found, about the nucleus, an indefinite number of somewhat larger bodies, which are also colourless and highly refractive; these are the pigment-bearers or CHROMATOPHORES (*ch*). NUCLEUS, CYTOPLASM, and CHROMATOPHORES, CONSTITUTE THE ELEMENTS OF THE LIVING BODY OF A TYPICAL VEGETABLE CELL. To designate all these collectively, it is customary to use the term PROTOPLASM, which is then to be understood as including all the living constituents of the cell or protoplast.

In animal cells modern investigations have revealed, in addition to the constituents of the protoplasm just mentioned, a small structure situated close to the nucleus, which has been termed the centrosome or attraction-sphere. Similar structures have been demonstrated in the lower cryptogamic plants (Fig. 57), but their existence in the cells of the higher Cryptogams and the Phanerogams is still a disputed point (17).

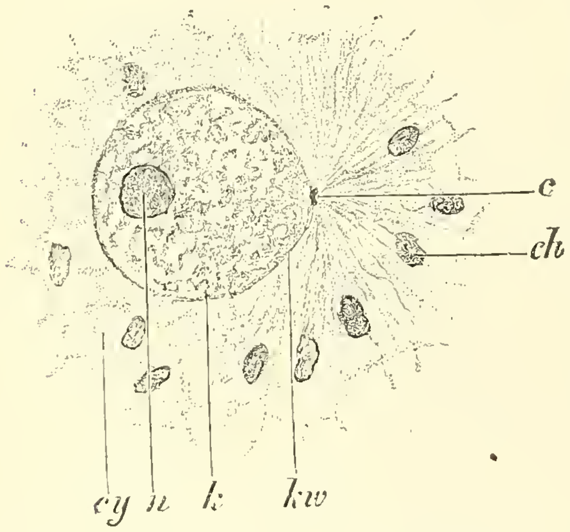


FIG. 57.—A nucleus of a cell of the young plant of *Fucus serratus*, a Brown Seaweed. *cy*, The surrounding cytoplasm; *k*, the nucleus; *kw*, nuclear membrane; *n*, nucleolus; *c*, centrosome; *ch*, chromatophores. (× 1000.)

The nucleus and cytoplasm are the two most essential constituents of the cell, and its vital functions depend on the interaction between them. In the lowest plants (*Cyanophyceae* and *Bacteria*) such a division of labour in the protoplasm is not certainly proved, a nucleus not having been as yet demonstrated in them (18). Chromatophores are wanting in the *Bacteria* and *Fungi*, as in all animal cells.

While animal cells usually remain continuously filled with protoplasm, vegetable cells soon form large SAP CAVITIES. It is only the embryonic cells of plants that are entirely filled with protoplasm, as the cells, for example, of an ovule or of a growing point; they afterwards become larger and contain proportionally less protoplasm. This can be seen in any longitudinal section through a stem apex. At a short distance from the growing point the enlarged cells have already begun to show cavities or VACUOLES (*v* in *A*, Fig. 58) in their cytoplasm. These are filled with a watery fluid, the CELL SAP. The cells continue to increase in size, and usually soon reach a condition in which their whole central portion is filled by a single, large sap cavity (*v* in *B*, Fig. 58). This is almost always the case when the increase in the size of the cell is considerable. The cytoplasm then forms only a thin layer lining the cell wall, while the nucleus takes a parietal position in the peripheral cytoplasmic layer. At other times, however, the sap cavity of a fully-developed cell may be traversed by bands and threads of cytoplasm; and in that case the nucleus is suspended in the centre of the cell. But whatever position the nucleus may occupy, it is always embedded in cytoplasm; and there is always an unbroken peripheral layer of cytoplasm lining the cell wall.

This cytoplasmic peripheral layer is in contact with the cell wall at all points, and, so long as the cell remains living, it continues in that condition. In old cells, however, this cytoplasmic layer frequently becomes so thin as to escape direct observation, and is not perceptible until some dehydrating reagent, which causes it to recede from the wall, has been employed. Such a thin cytoplasmic peripheral layer has been described by HUGO V. MOHL under the name of PRIMORDIAL UTRICLE.

Dead cells lose their living protoplasmic contents, and, strictly speaking, should no longer be termed cells, although the name was first applied to them when in that condition. In reality they represent only cell cavities. With their death, however, cells do not lose their importance to a plant. Without such cell cavities a plant could not exist, as they perform for it the office of water-carriers, while at the same time exercising other functions. The necessary rigidity of a plant is also dependent, to a great extent, on the mechanical support afforded by a framework composed of dead cells. Thus the heart of a tree consists exclusively of the walls of dead cells.

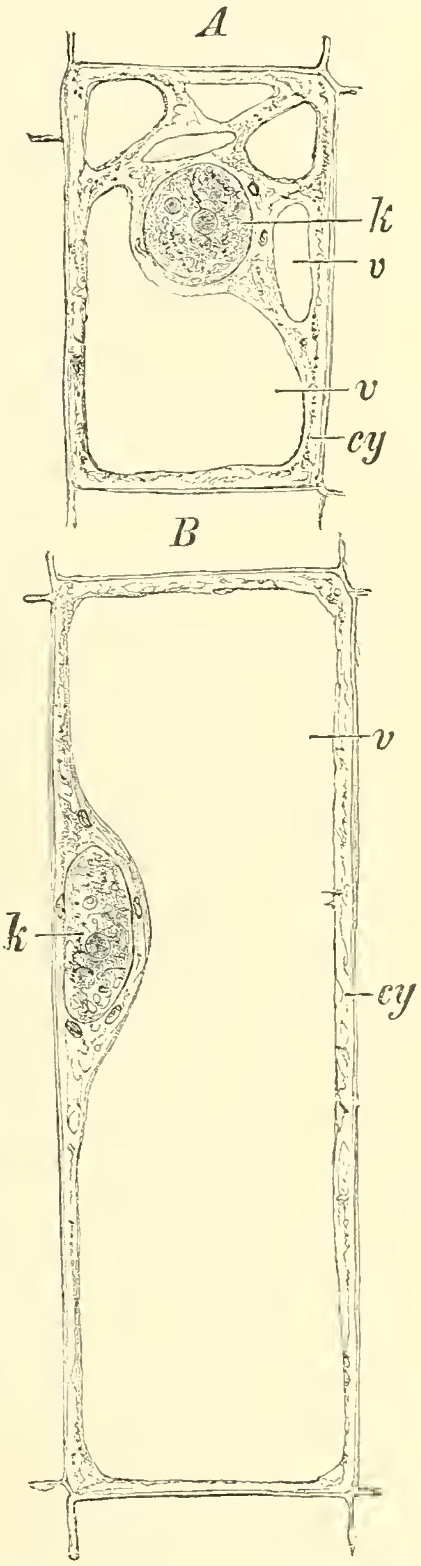


FIG. 58.—Two cells taken at different distances from the growing point of a phanerogamic shoot. *k*, Nucleus; *cy*, cytoplasm; *v*, vacuoles, represented in *B* by the sap cavity. (Somewhat diagrammatic, × circa 500.)

The Protoplasm.—In order to facilitate an insight into the real character of protoplasm, attention will first be directed to the SLIME FUNGI or fungus animals (*Myxomycetes*), a group of organisms which stand on the border between the animal and vegetable kingdoms. These Myxomycetes are characterised at one stage of their development by the formation of a PLASMODIUM, a large naked mass of protoplasm.

The plasmodium is formed from the protoplasm of the spores. These spores are unicellular bodies (Fig. 59, *a*, *b*), filled with cytoplasm, in which lies a central nucleus, and are surrounded by firm cell walls. The spores germinate in water, their contents, breaking through the spore walls, come out (*c*, *d*) and round themselves off. A change of form soon takes place; the protoplasmic mass elongates and assumes somewhat the shape of a pear, with the forward end prolonged into a fine whip-like process or flagellum (*e*, *f*, *g*). Thus the contents of the spore have become transformed into a SWARM-SPORE, which now swims away by means of whip-like movements of its flagellum.

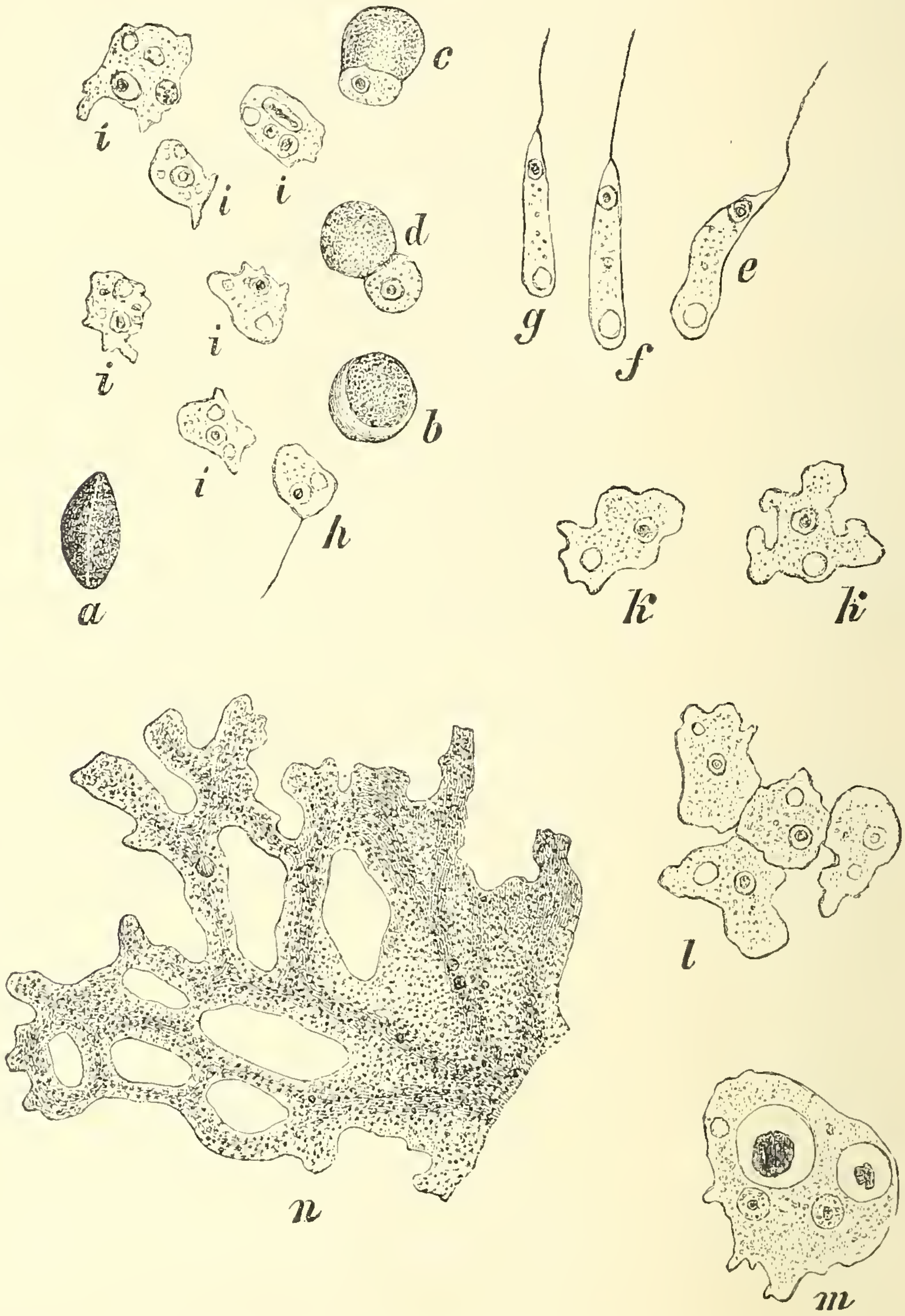


FIG. 59.—*Chondrioderma difforme*. *a*, Dry, shrivelled spore; *b*, swollen spore; *c* and *d*, spores showing escaping contents; *e*, *f*, *g*, swarm-spores; *h*, swarm-spore changing to a myxoamœba; *i*, younger, *k*, older myxoamœba; *l*, myxoamœbæ about to fuse; *m*, small plasmodium; *n*, portion of fully-developed plasmodium. (*a*-*m*, × 540 : *n*, × 90.)

In addition to the nucleus, which is visible in the front end of every swarm-spore, a vesicle may be seen at the other end, which, after gradually increasing in size, suddenly vanishes, only to swell again into view. This vesicle is a CONTRACTILE VACUOLE. The presence of such a contractile vacuole in an organism was formerly considered a certain indication of its animal nature. Now, however, contractile vacuoles have been observed in the swarm-spores of many green Algæ, of whose vegetable nature there can be no doubt.

The swarm-spores of the Myxomycetes soon lose this characteristic swarm-movement, draw in their flagella, and pass into the amœba stage of their development, in which, like animal amœbæ, they assume irregular, constantly changing shapes, and are capable of performing only amœboid creeping movements. In the case of *Chondrioderma difforme*, a Myxomycete of frequent occurrence in rotting parts of plants (Fig. 59), a number of the amœbæ eventually collect together (*l*) and coalesce. In this way, as is also the case with most other Myxomycetes, the amœbæ ultimately give rise to a plasmodium (*n*).

Although each one of the amœbæ is so small that it can only be seen with the aid of a microscope, the plasmodium into which they become united may attain a size large enough to be measured in centimetres.

The cytoplasm, both of the single amœba and of the plasmodium, consists of a clear ground substance, through which granules are distributed. This substance is of the consistence of a tenacious fluid; its superficial region is denser and free from granules, while these are numerous in the less dense central portion. The granules enable the internal streaming movements of the cytoplasm to be recognised. The currents are constantly changing their direction, moving either towards or away from the margin. The formation and withdrawal of processes of the margin stand in relation to the direction of the currents. When naked masses of protoplasm such as these plasmodia encounter foreign bodies, they can enclose them in vacuoles, and, when of use as food, digest them.

Deprived of its component water the protoplasm becomes hard and tenacious, and, without losing its vitality, ceases to perform any of its vital functions until again awakened into activity by a fresh supply of water. In case of a scarcity of water the plasmodia of the Myxomycetes may form SCLEROTIA, that is, masses of resting protoplasm of an almost wax-like consistency. Months and indeed sometimes years afterwards, it is possible for such sclerotia, if water be properly supplied, to again produce motile plasmodia. Similarly, in seeds kept for a long time, the protoplasm consolidates into a hard mass, which may be easily cut with a knife, while the nuclei will be found to have shrunk and lost their original shape. Nevertheless the protoplasts, after absorbing water, may return again to a condition of activity.

Protoplasm is not a simple substance chemically; it consists rather of different components, which are subject to continual change. Treated as a uniform mass, protoplasm always gives a proteid reaction; when incinerated, fumes of ammonia are given off.

Active protoplasm generally gives an alkaline, and, under certain conditions, a neutral reaction, but never an acid one. The protoplasm of the higher plants coagulates at a temperature not much over 50° C., in the Schizophytes, however, usually not below 75° C. In a state of inactivity, as in spores and seeds, it can endure a still higher temperature without coagulating; when coagulation has once taken place, death ensues. The spores of many Bacteria can withstand a temperature as high as 105° C. Treated with alcohol or ether, or with acids of definite concentrations, with bichromates of the alkali metals, or with corrosive sublimate, protoplasm quickly coagulates, while at the same time insoluble proteid compounds are formed. Coagulating reagents, accordingly, play an important part in microscopic technique; of especial value are such which, while fixing and hardening the protoplasm, change its structure in the least degree. As a fixing and hardening reagent for vegetable tissues, alcohol is particularly serviceable; under certain conditions, sublimate alcohol, or 1 to 2 per cent formaldehyde. For animal cells and for the lower plants, 1 per cent chromic acid, 1 per cent acetic acid, 0·5 to 1 per cent osmic acid, concentrated picric acid, or corresponding mixtures of these acids, and also formaldehyde, are used for the same purpose. Iodine stains protoplasm brownish yellow; nitric acid, followed by caustic potash, yellowish brown (xanthoprotein reaction); sulphuric acid, if sugar be present, rose red. Acid nitrate of mercury (MILLON's reagent) gives to protoplasm a brick-red colour. These reactions occur with all proteid substances though they are not absolutely distinctive of them. Protoplasm is soluble in dilute caustic potash and also in eau de Javelle (potassium-hypochlorite), and accordingly both of these reagents may be recommended for clearing specimens, when the cell contents are not to be investigated. All of the above-mentioned reagents kill protoplasm; until they have done so, their characteristic reactions are not manifested. A large number of albuminous bodies or albuminates have been named which are said to enter into the composition of living protoplasm. It is worthy of note that most of these compounds, although still not fully determined, contain phosphorus. Such as are peculiar to the nucleus have been comprehended under the term NUCLEIN. Staining reagents have also become an important help to microscopic investigations for determining the composition of protoplasm. This is due to the fact that the different constituents of protoplasm take up and retain the stain with different degrees of intensity and energy. As a general rule, only coagulated protoplasm can absorb colouring matter, although some few aniline stains can, to a limited extent, permeate living protoplasts. For staining vegetable protoplasts, which have been previously hardened, the various carmines, hæmatoxylin, iodine green, acid fuchsin, eosin, methylene blue, and aniline blue, gentian-violet and orange, have been found particularly convenient. The different components of the protoplasm absorb the stains with different intensities, and, when reagents are employed to remove the colouring matters, they exhibit differences in their power to retain them. The nucleus generally becomes more intensely coloured than the rest of the protoplasm, especially a part of its substance, which is therefore called CHROMATIN. In addition to those substances, which are to be regarded as integral parts of active protoplasm, it always includes derivative products of albuminates, particularly amides, as asparagin, glutamin; also ferments as diastase, pepsin, invertin; at times alkaloids, and always carbohydrates and fats. The ash left after incineration also shows that protoplasm always contains mineral matter, even if only in small quantities. All substances which, as such, do not enter directly into the composition of protoplasm, but are only included within it, are designated by the term METAPLASM.

The Cytoplasm.—The cytoplasm of vegetable cells, which possess a cell wall, is like that of the amœbæ and plasmodia of Myxomycetes (p. 55), a tenacious fluid. It partakes of the physical properties of fluids, and on being artificially freed from the cell wall, tends to assume the spherical form. Its cohesion appears to be greater in merismatic cells than in those which are older, while in certain cases a still firmer consistence may be attained as in the cilia borne by swarm-spores.

Both in the case of the Myxomycete and of the vegetable cell enclosed by a wall, the basis of the cytoplasm consists of a hyaline substance termed the hyaloplasm. When granules are distributed through the cytoplasm it is spoken of as granular plasma. An extremely thin boundary layer is found at the periphery of the cytoplasm, which is quite free from granules, and a similar layer bounds every vacuole present in the cytoplasm. The wall of the vacuole is characterised by a greater tenacity of life than the rest of the cytoplasm, remaining alive for some time after the latter has been killed by the action of a 10 per cent solution of potassium nitrate. Since the vacuole wall regulates the pressure exerted by the cell sap contained in the vacuole, Hugo de Vries has applied the name TONOPLAST (19) to this layer.

The small bodies distributed through the granular plasma consist of various substances, and may be classed together as microsomes. Some of them are small cavities filled with dissolved substances, and to these the name physodes has been given.

Even though bounded by a cell wall the cytoplasm frequently exhibits movements comparable to those of the naked amœbæ and plasmodia of Myxomycetes. The study of the movements in the latter group showed that various kinds of movement could be distinguished; the waving movement of the flagellum of the swarm-spore, the change in external form of amœbæ and plasmodia, to which their power of creeping about is due, and finally a streaming movement in the cytoplasm. The movement in cells provided with walls is mostly found in those which have advanced somewhat from the young condition. The cytoplasm may either exhibit isolated streaming movements, the direction of which may undergo reversals, or a single stream, the direction of which is constant. These two forms of movement are distinguished as CIRCULATION and ROTATION respectively. In rotation, which is found in cells with the cytoplasm reduced to a layer lining the wall, the single continuous current follows the cell wall. In circulation, on the other hand, the layer of cytoplasm lining the wall takes no part in the movement, which is found in the strands traversing the vacuole. Circulation is common in cells of land-plants, while rotation is more usual in water-plants. The stimulus caused by wounding the tissues in making the preparation frequently increases the activity of the movement.

A particularly favourable object for the study of protoplasm in circulation is afforded by the staminal hairs of *Tradescantia virginica.* In each cell (Fig. 60) small, fine currents of protoplasm flow in different directions in the peripheral cytoplasmic layer, as well as in the cytoplasmic threads, which penetrate the sap cavity. These cytoplasmic threads gradually change their form and structure, and thus alter the position of the cell nucleus.

When the protoplasm is in rotation, the cell nucleus and chromatophores are usually carried along by the current, yet there may be an outer layer of granular plasm which remains motionless and retains the chromatophores. This is the case with the Stoneworts (*Characeae*), whose long internodal cells, especially in the genus *Nitella*, afford good examples of well-marked rotation.

Properly fixed cytoplasm exhibits, more or less clearly, a honeycomb-like structure; sometimes fibrillæ (Fig. 57) can also be distinguished in it. Thus there appear to be two constituents of the general cytoplasm, one of which tends to form foam-like alveoli, the other to become differentiated into fibrillæ.

These two constituents may be distinguished as alveolar plasma and fibrillar plasma respectively. Since it would appear that the former is especially concerned with the nutritive processes, while the fibrillar plasma influences the process of development, they may also be termed trophoplasm and kinoplasm; the latter has also been called archeplasm. When traced to their origins the limiting layer of the cytoplast is found to belong to the kinoplasm, the walls of vacuoles to the trophoplasm. The vacuoles arise by interspaces of the alveolar plasma enlarging and fusing with one another.

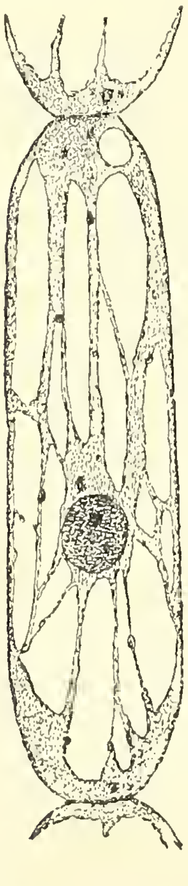


FIG. 60.—Cell from a staminal hair of *Tradescantia virginica*, showing nucleus suspended by protoplasmic strands. (× 240.)

The Cell Nucleus.—The nucleus appears to be made up of threads twisted together and forming an anastomosing network (Fig. 56), which, however, in living objects can only be distinguished by the punctated appearance it gives to the nucleus. Streaming movements do not take place within the nucleus. An insight into the nuclear structure is only to be attained with the help of properly fixed and stained preparations. It is then possible to determine that the greater part of this nuclear network is composed of delicate and, for the most part, unstained threads, in which lie deeply stained granules. The substance of the threads has been distinguished as LININ (*l*), that of the granules as CHROMATIN (*ch*). One or more large nuclear bodies, or nucleoli (*n*), occur at the intersections of some of the linin threads, which, although deeply stained, have not taken the same tint as the chromatin granules. The network of the nucleus lies within the NUCLEAR CAVITY, which is filled with nuclear sap and surrounded by a membrane (*w*). Although this is generally spoken of as the nuclear membrane, strictly speaking it is a part of the surrounding cytoplasm, and is the protoplasmic layer or pellicle with which the cytoplasm separates itself from the nuclear cavity. The nucleus in young cells with abundant protoplasm is, as a rule, spherical. When situated in the lining layer of cytoplasm of older cells, it is frequently of a flattened form, while in elongated cells it exhibits a corresponding elongation. Exceptionally in old cells the nucleus is forked, lobed, or of some other irregular shape. These changes in form of the nucleus are due to slow movements, which cannot, as a rule, be directly observed.

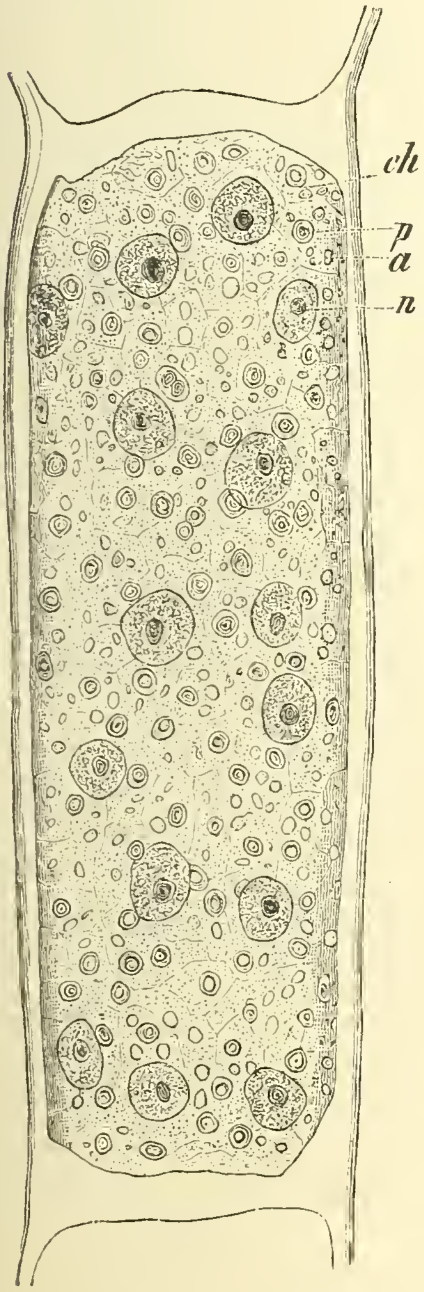


FIG. 61.—A cell of *Cladophora glomerata*, fixed with 1 per cent chromic acid and stained with carmine. *n*, Nuclei; *ch*, chromatophores; *p*, pyrenoids; *a*, starch grains. (× 540.)

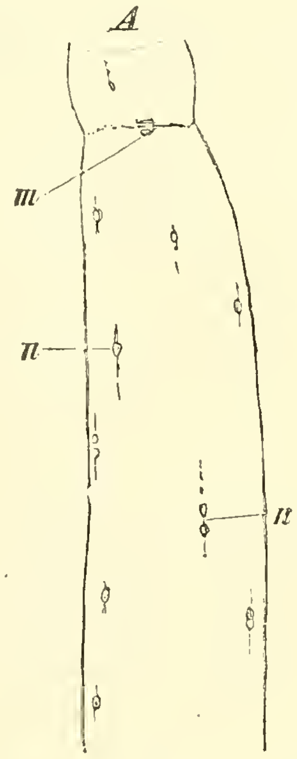


FIG. 62.—Portions of two adjacent cells in a hypha from the stalk of *Psalliota arvensis*. *n*, Nuclei; *m*, pits. (× 540.)

While the cells of the Cormophytes are almost exclusively uninuclear, in the Thallophytes, on the contrary, multinuclear cells are by no means infrequent. In the Fungi, and in the *Siphoneae* among the Algæ, they are the rule. The whole plant is thus composed either of but one single multinuclear cell, which may be extensively branched (Fig. 253), or it may consist of a large number of multinuclear cells, forming together one organism. Thus, after suitable treatment, several nuclei may be detected in the peripheral cytoplasm in the cells of the common filamentous fresh-water Alga *Cladophora glomerata* (Fig. 6, p. 12), (Fig. 61).

The nuclei of the long, multinuclear cells (Fig. 62, *n*) of fungoid filaments, or HYPHÆ, and also of many *Siphoneae*, are characterised by their diminutive size.

The Centrosomes.—These bodies, which are of general occurrence in animal cells, have been successfully demonstrated in a number of the lower Cryptogams (Thallophytes and Bryophytes). They are, as a rule, very small (Fig. 57), only attaining a somewhat more considerable size in some Fungi. Hitherto centrosomes have not been shown to exist in the cells of more highly organised plants. Structures similar to them, however, appear in the development of the motile male sexual products in Pteridophytes and some Gymnosperms (20), and take part in the construction of the spermatozoid.

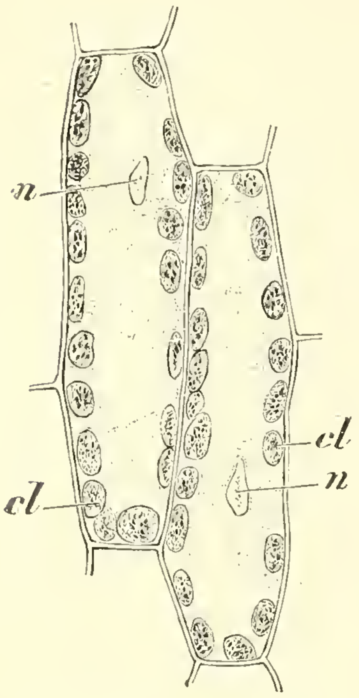


FIG. 63.—Two cells from a leaf of *Funaria hygrometrica*. *cl*, Chloroplasts; *n*, nucleus. (× 300.)

The Chromatophores (21).—In the embryonic cells of growing points, where the chromatophores (Fig. 56, *ch*) are principally located around the nucleus, they first appear as small, colourless, highly refractive bodies; and in the embryonic cells of ovules they have a similar appearance. They may retain the same appearance in older cells (Fig. 110, *A*, *l*), but in them they also attain a further development, as CHLOROPLASTS, LEUCOPLASTS, or CHROMOPLASTS. Since these bodies have the same origin they are all included in the one term, CHROMATOPHORES.

In parts of plants which are exposed to the light the chromatophores usually develop into chlorophyll bodies or CHLOROPLASTS. These are generally green granules of a somewhat flattened ellipsoidal shape (Fig. 63), and are scattered, in great numbers, in the parietal cytoplasm of the cells. All the chloroplasts in the Cormophytes and, for the most part also, in the green Thallophytes present this same granular form. In the lower Algæ, however, the chlorophyll bodies may assume a band-like (Fig. 240, *C*), stellate or tabular shape. The fundamental substance of the chlorophyll bodies is itself colourless, but contains numerous coloured drops, which are termed GRANA. These consist of an oleaginous substance, which holds in solution one or two green pigments (chlorophyll and allochlorophyll), and two yellow pigments (chrysophyll and xanthophyll). These colouring substances may be extracted by means of alcohol, leaving only the colourless plasmic substance of the chlorophyll body remaining.

The easiest way in which a solution of chlorophyll can be prepared, is to extract the chlorophyll by means of alcohol from green leaves that have been previously boiled in water. The green chlorophyll pigment is also soluble in ether, fatty and ethereal oils, paraffine, petroleum, and carbon disulphide. The alcoholic solutions appear green in transmitted light; blood red in reflected light, on account of fluorescence. When an alcoholic solution of chlorophyll is shaken up with benzole, the latter on standing rises to the surface as a green solution, leaving the alcohol yellow.

If a ray of sunlight be made to pass through a tolerably thick layer of an alcoholic solution of chlorophyll, and then decomposed by a prism, the resulting spectrum will show seven absorption bands (Fig. 64). The darkest band extends from FRAUNHOFER's line, *B*, to some distance beyond the line *C*. The other bands are not so intense: one lies between *C* and *D*, another near *D*, and one near *E*, while the other three bands are broader and cover almost the whole blue half of the spectrum.

According to recent investigations by Marchlewski and Schunck (22) the two green pigments named above are to be detected in the alcoholic extract from leaves. The one, true chlorophyll, is always present; the other, which has been termed allochlorophyll, cannot be detected in some plants. True chlorophyll is characterised by three absorption bands in the less refrangible half of the spectrum, and three in the more refrangible portion. As yet only one band, which lies in the red portion of the spectrum and coincides with the first absorption band of chlorophyll, is known for allochlorophyll. C. A. Schunck (23) has obtained one of the yellow pigments (chrysophyll) as shining red crystals, while xanthophyll forms amorphous masses. The amount of chlorophyll in a green plant is very small. TSCHIRCH (24) has calculated that out of a square metre of green foliage leaves only from 0·2 to 1·0 gram of chlorophyll can be obtained. Acids decompose chlorophyll; contact even with the acid cell sap is sufficient to change the colour of the chlorophyll bodies to a brownish green. It is due to this fact that a plant turns brown when dried.

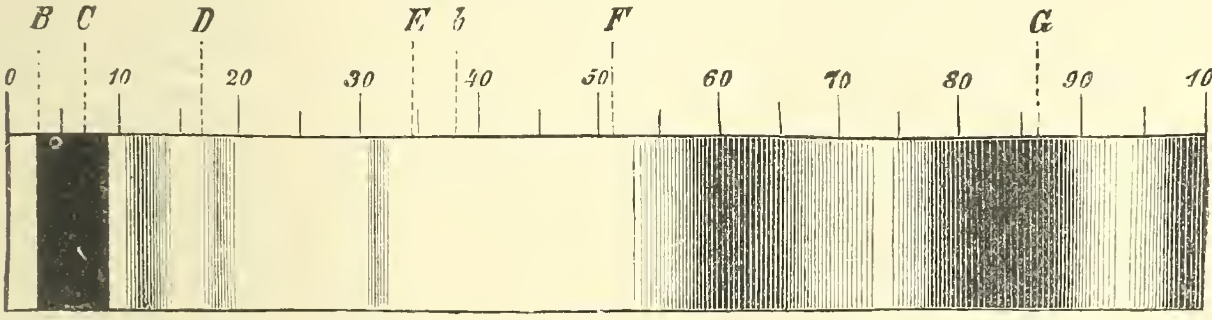


FIG. 64.—Spectrum of an alcoholic solution of chlorophyll extracted from foliage leaves. (After KRAUS.) The absorption bands in the less refractive part of the spectrum (*B*-*E*) are given by a concentrated solution, those in the more highly refractive part of the spectrum by a dilute solution.

From the investigations of Marchlewski and Nencki it appears that a relationship exists between chlorophyll and hæmoglobin (the pigment contained in red blood corpuscles), a fact of the greatest theoretical importance (25).

The green colour of the chlorophyll in some groups of Algæ is more or less masked by other pigments. In addition to the chlorophyll green, with its accompanying yellow and orange-red pigments, many of the blue-green *Schizophyceae* contain a blue colouring matter, phycocyanin; the brown Algæ, a brown pigment called phycophæin; while the red Algæ possess a red pigment termed phycoerythrin. These pigments, which are peculiar to Algæ, are soluble in water, and are characterised by a beautiful fluorescence. The phycocyanin may often be found as a blue border surrounding a blue-green Fission-Alga which has been dried in a press. Red seaweeds washed up by the ocean soon become green, as, owing to the rapid decomposition of the phycoerythrin, the chlorophyll is no longer concealed.

Before leaves fall in the autumn, their cells lose almost all of their cytoplasmic contents, and at the same time the chloroplasts undergo disorganisation. There remains only a watery substance in the cell cavity, in which a few oil globules and crystals, together with a few yellow, strongly refractive bodies, can be seen. Sometimes this liquid in the cell cavities becomes red, and thus imparts to the foliage its autumnal brilliancy. In the leaves of coniferous trees, which only indicate the approaching winter by assuming a somewhat brownish tint, the case is different. The chlorophyll-green of their chloroplasts changes to a brownish green, but in the following spring regains its characteristic colour.

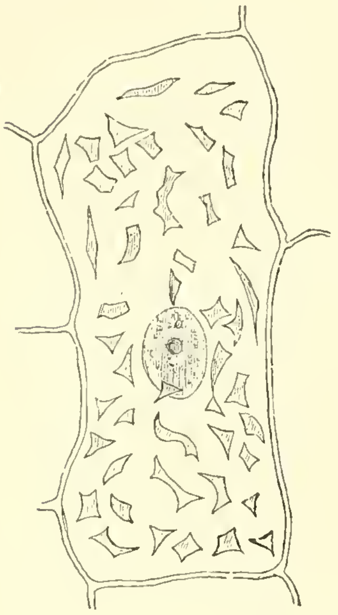


FIG. 65.—Cell from the upper surface of the calyx of *Tropaeolum majus*, showing chromatophores. (× 540.)

In such phanerogamic parasites or humus-plants as are devoid of green colour, the chloroplasts either do not develop, or they are white, or have only a brownish or reddish colour. No chromatophores are found in the Fungi.

In the interior of plants, where light cannot penetrate, LEUCOPLASTS are developed instead of chloroplasts from the rudiments of the chromatophores. They are of a denser consistency than the chloroplasts, and resembling a flattened ellipsoid in shape, are often somewhat elongated in consequence of enclosed albuminous crystals. If the leucoplasts become at any time exposed to the light, they not infrequently change into chloroplasts. This frequently occurs, for example, in potatoes.

The CHROMOPLASTS of most flowers and fruits arise either directly from the rudiments of colourless chromatophores, or from previously formed chloroplasts. In shape the chromoplasts resemble the ellipsoidal granules of the chloroplasts, except that they are usually smaller; or, in consequence of the crystallisation of their colouring pigment, they assume a triangular, tabular, needle, or fan-shaped form (Figs. 65, 66). The colour of the chromoplasts varies from yellow to red, according to the predominance of xanthophyll or carotin. The name carotin has been derived from the Carrot (*Daucus Carota*), in the roots of which it is particularly abundant (Fig. 66). The frequent crystalline form of the chromoplasts is, in a great part, due to the tendency of carotin to crystallisation, although it may be also occasioned by needle-like crystals of albumen. Xanthophyll, however, is never present in the chromoplasts except in an amorphous condition.

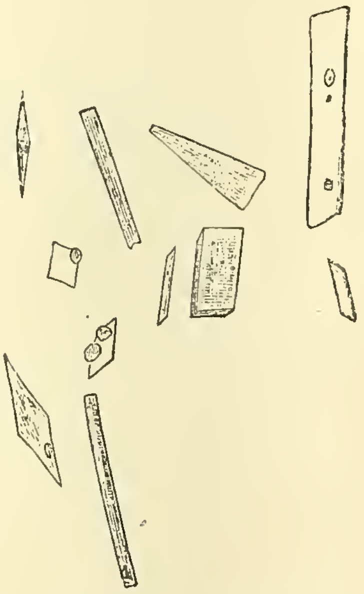


FIG. 66.—Chromoplasts of the Carrot, some with starch grains. (× 540.)

Origin and Structure of the Cell Wall (^{26}).—The membrane which encloses the vegetable protoplast is a product of the protoplasm. Many low organisms belonging to the Algæ liberate naked protoplasts from their cells; these swarm-spores (Fig. 96, *A*) serve to multiply the plant vegetatively. They soon settle down and form a thin cell membrane on the surface of the protoplast. The possession of this wall gives to the cell, which before resembled an animal cell, its distinctively vegetable character. Usually the spore proceeds to grow into a filament. Naked motile spores are not found in the more highly organised plants. In them, however, the ovum, from which the development starts, has no cell wall until it has been fertilised; from this stage on all the cells composing the plant are surrounded by cell walls. At the growing points of plants the cells are separated from one another only by extremely thin membranes or cell walls. The rapid growth in length which sets in a short distance from the growing point, as a result of the increase in the size of the cells, must be accompanied by a corresponding GROWTH IN SURFACE of the cell walls. So long as this growth in surface continues, the cell walls remain thin. After the cells have attained their ultimate size, the GROWTH IN THICKNESS of the cell walls then begins. The growth in surface of the cell wall may either involve the introduction of new material, or may take place without this. In the latter case the membrane would become thinner if new lamellæ were not simultaneously

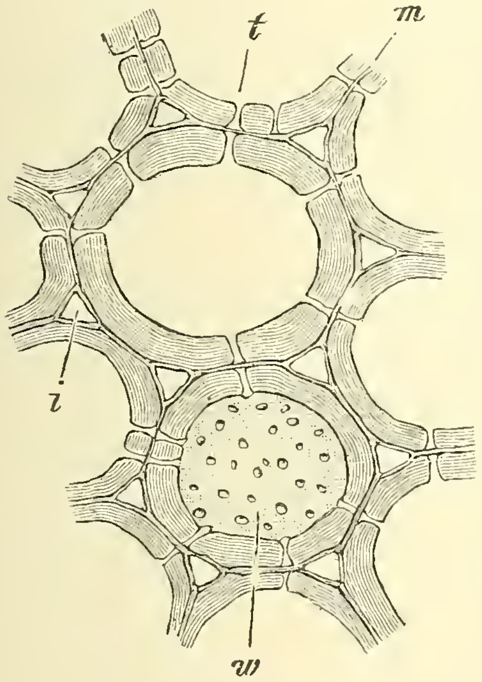


FIG. 67.—Strongly thickened cell from the pith of *Clematis vitalba*. *m*, Middle lamella; *i*, intercellular space; *t*, pit; *w*, pitted transverse cell wall. (× 300).

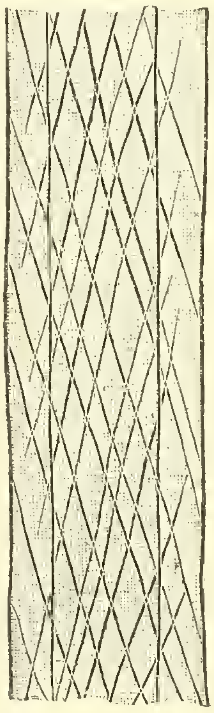


FIG. 68.—Part of a sclerenchymatous fibre from *Vinca major*. The striations of the outer layers are more apparent than those of the inner layers. The walls, as seen in optical section, are also shown. (× 500.)

applied to its surface. Growth of the wall by the introduction of new particles between those previously existing is termed GROWTH BY INTUSSUSCEPTION, while that which occurs by the laying down of new lamellæ on the surface of the older ones is called GROWTH BY APPOSITION. The growth in thickness of most cell walls takes place by apposition, and thus the stratification, which such thickened walls exhibit, is brought about (Fig. 67). Thicker, dense layers alternate with thinner less dense ones. The denser layers can be recognised by their high refractive power. In many cases lamellæ, deposited by apposition, become further thickened and otherwise modified by a process of intussusception. Three distinct layers can frequently be distinguished in strongly thickened cell walls, such as those of the wood, a primary, a secondary, and a tertiary thickening layer; these differ in their optical appearance and their chemical composition. The secondary thickening layer is usually the most strongly developed, and forms the chief part of the cell wall. The tertiary or inner layer is thinner and more highly refractive.

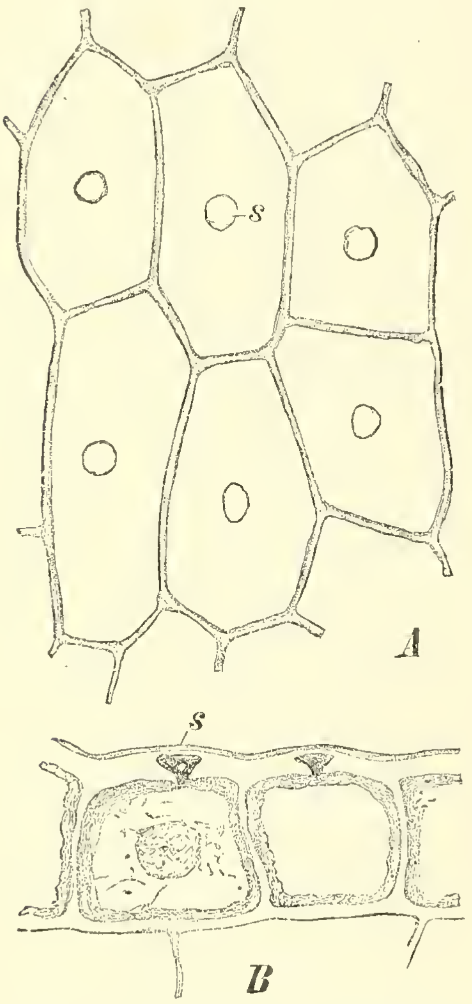


FIG. 69.—*A*, Surface view of cells from the sensitive side of the tendril of *Cucurbita Pepo*, showing tactile pits, *s*. *B*, Transverse section through similar cells, a small crystal of calcium oxalate is present in the pit. (× 450.)

Thicker cell walls or layers of the wall which appear homogeneous frequently exhibit a stratification when treated with strong acids or alkalis. In many cases the thickening layers exhibit delicate striations in surface view. The striations extend through the whole thickness of the layers, usually running obliquely to the long axis of the cell, and often crossing one another in the different thickening layers (Fig. 68). In special cases, but only in the formation of reproductive cells, an inner thickening layer, completely detached from the others, is produced, as in the formation of pollen grains and spores, which, enclosed only by this inner membrane, finally become freed from the older thickening layer. This process is often alluded to as REJUVENESCENCE; in such cases, it should be noted, there are, in reality, no new cells formed.

The thickening of the cell wall seldom takes place uniformly over the whole surface; but some portions are thickened, while, at other points, the original or primary cell wall remains unchanged. In this way pores are formed which penetrate the thickening layers. These pores or PITS may be either circular (Figs. 67, *w*, 71, *m*), elliptical, or elongated. The pits in adjoining cells converge, and would form one continuous canal, were it not that the unthickened primary cell wall persists as a CLOSING MEMBRANE between two converging pits. As a result of the continued thickening of the cell wall, the canals of several pits often unite, and so BRANCHED PITS are formed. Such branched pits have usually very narrow canals, and occur for the most part only in extremely thick and hard cell walls, as, for instance, in those of the

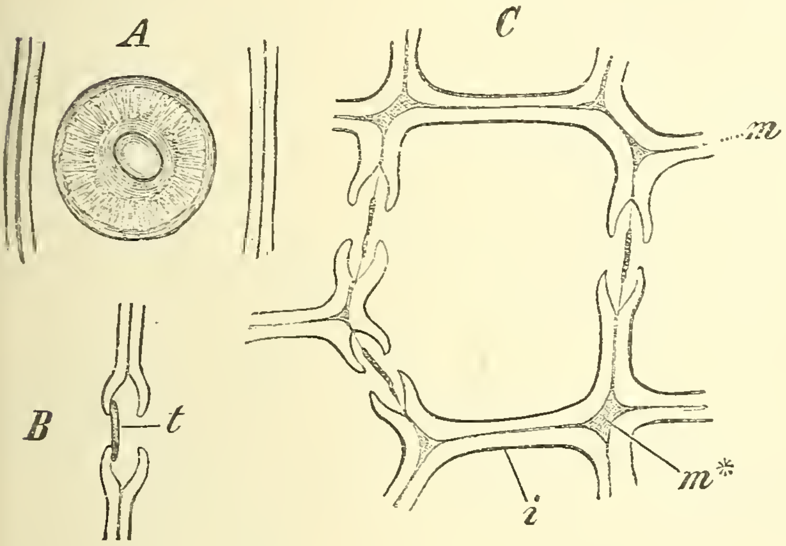


FIG. 70.—From the wood of the Pine, *Pinus sylvestris*. *A*, Bordered pit in surface view; *B*, bordered pit in tangential section; *t*, torus; *C*, transverse section of a tracheid; *m*, middle lamella, with gusset, *m**; *i*, inner peripheral layer. (× 540).

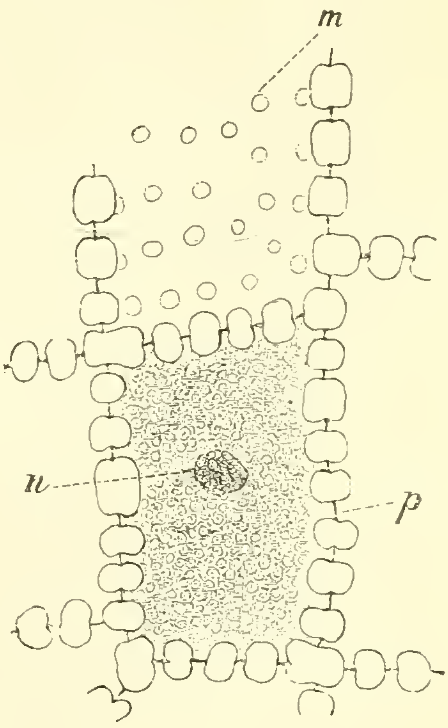


FIG. 71.—Cells from the endosperm of *Ornithogalum umbellatum*. *m*, Pits in surface view; *p*, closing membrane; *n*, nucleus. (× 240.)

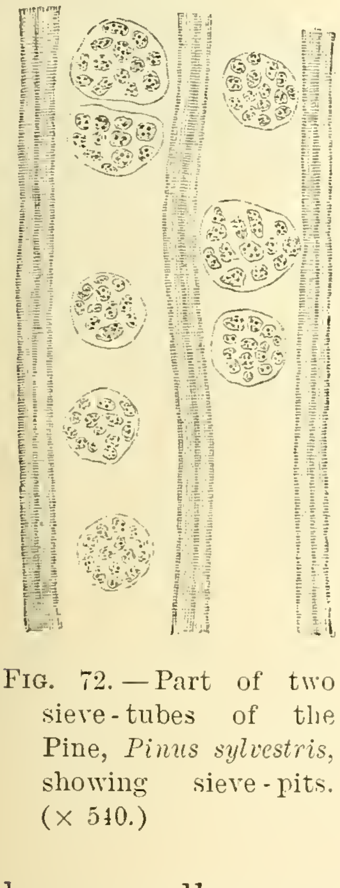


FIG. 72.—Part of two sieve-tubes of the Pine, *Pinus sylvestris*, showing sieve-pits. (× 540.)

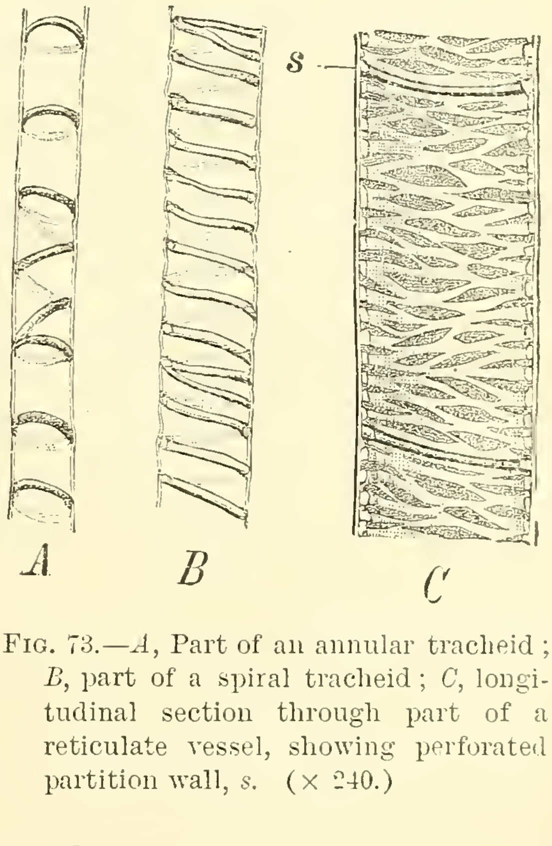


FIG. 73.—*A*, Part of an annular tracheid; *B*, part of a spiral tracheid; *C*, longitudinal section through part of a reticulate vessel, showing perforated partition wall, *s*. (× 240.)

so-called sclerotic cells or sclereids. Simple pits may, on the other hand, expand on approaching the primary cell wall.

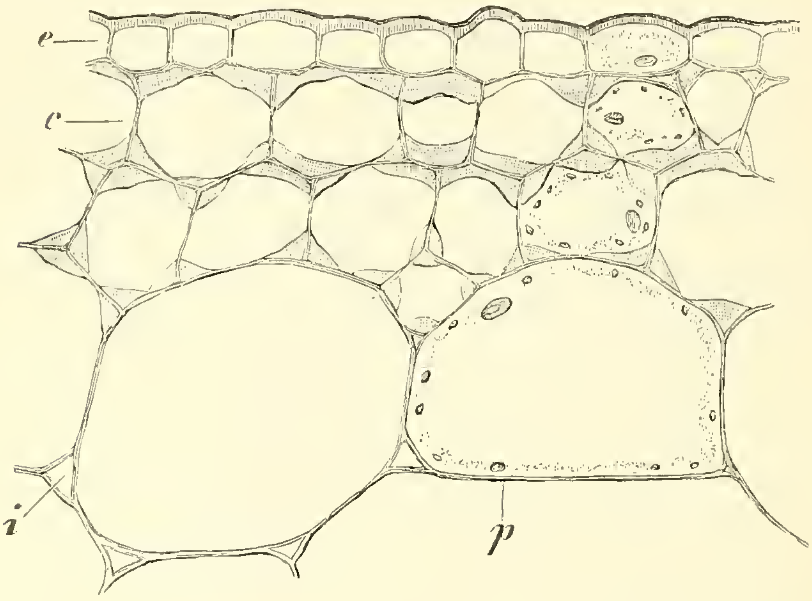


FIG. 74.—Part of transverse section of a stem of *Impatiens parviflora*. *e*, Epidermis; *c*, collenchyma; *p*, thin-walled parenchymatous cells; *i*, intercellular space. (× 300.)

Pits widened towards the membrane are found in the external cell walls of many tendrils (27). These pits, which are filled with cytoplasm, probably receive the stimulus, and may be termed tactile pits (Fig. 69). The structures known as BORDERED PITS (Fig. 70) are but a special form of expanded simple pits. The pit may be present on one or both sides of the wall; the former is the case when the water-conducting element abuts on a cell with protoplasmic contents, the latter when the pitted wall separates two water-conducting elements. In bordered pits the closing membrane is thickened at the centre to form a TORUS (Fig. 70, *C*). By the curving to one side or the other of the closing membrane, the torus may so act as to close the pit canal (Fig. 70, *B*). Bordered pits are only formed in cells which are soon to lose their living contents and thus serve merely as channels for conducting water. The bordered pits apparently act as valves. Seen from the surface a bordered pit appears as two concentric rings (Fig. 70, *A*). The smaller, inner ring represents the narrow opening of the pit into the cell cavity; the larger, outer ring indicates the junction of the wall of the PIT CHAMBER with the primary cell wall.

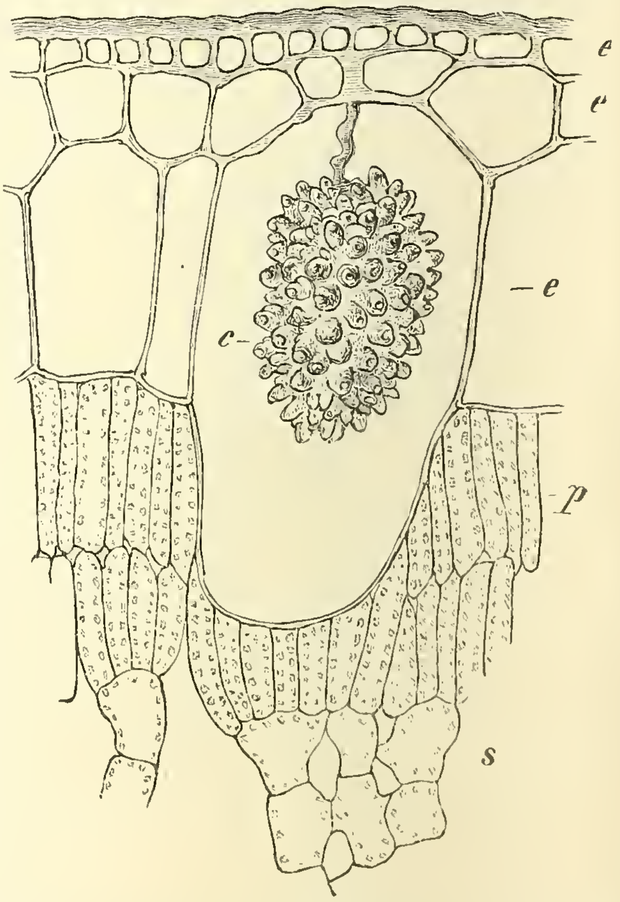


FIG. 75.—Part of transverse section of a leaf of *Ficus elastica*. *c*, Cystolith; *e*, *e*, *e*, triple-layered epidermis; *p*, palisade parenchyma; *s*, spongy parenchyma. (× 240).

Very large pits between adjoining living cells have often thin places in their closing membrane, and are then spoken of as compound pits. A special example of such pits is afforded by the SIEVE-PITS, in which the closing membrane, in that case called the SIEVE-PLATE, is perforated by fine openings or pores (Fig. 72).

In cases where the greater part of the cell wall remains unthickened, it is characterised rather by a description of its thickened than unthickened portions; it is in this sense that the terms annular, spiral, and reticulate are used (Fig. 73). Just as in the case of cells with bordered pits, annular, spiral, and reticulate cell walls are only acquired by cells that soon lose their contents, and act in the capacity of water-carriers. Such wall thickenings serve as mechanical supports, to give rigidity to the cells, and to enable the cell walls to withstand the pressure of the surrounding cells.

The thickened bands by which such thickenings of the cell wall are effected are attached by narrowed bases to the primary membrane (28). When the membrane separates two water-conducting elements its central portion is thickened like the torus of the bordered pit. The annular and spiral types of thickening characterise the water-conducting elements of growing parts of the plant, since they allow of corresponding extension of the wall. The thickening band can often be removed as a continuous spiral from the lamella to which it is attached.

COLLENCHYMATOUS cells are living cells, the walls of which are thickened principally at the corners (Fig. 74, *c*). Cells on the surface of plants have usually only their outer walls thickened (Fig. 74, *e*).

By the thickening of cell walls at special points, protuberances projecting into the cell cavity are formed; in this way the formations known as CYSTOLITHS arise. Certain large cells in the leaves of the Indiarubber plant (*Ficus elastica*) contain peculiar clustered bodies, formed by the thickening of the cell wall at a single point (Fig. 75). In their formation a stem-like body or stalk first protrudes from the cell wall; by the addition of freshly-deposited layers this becomes club-shaped, and, by continued irregular deposits, it finally attains its clustered form.

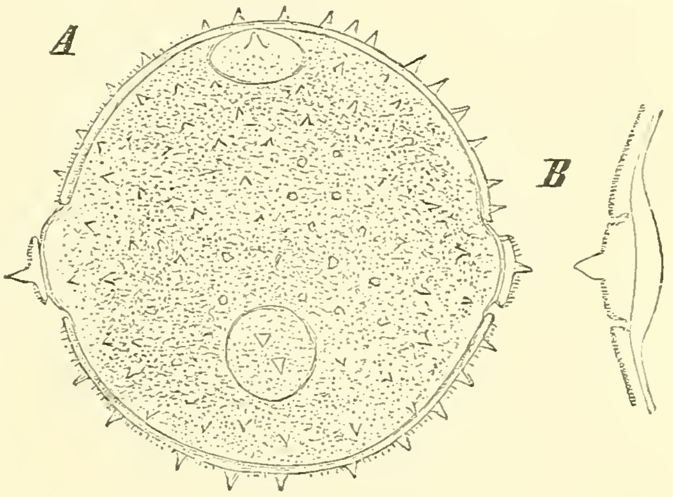


Fig. 76.—*A*, Pollen-grain of *Cucurbita Pepo* in surface view, and partly in optical section, rendered transparent by treating with oil of lemons (× 240); *B*, part of transverse section of pollen grain of *Cucurbita verrucosa* (× 540.)

So far only centripetal wall thickenings have been described. Cells, the walls of which are centrifugally thickened, can naturally only occur where the cell walls have free surfaces. The outer walls of hairs generally show small inequalities and projections. The surface walls of spores and pollen grains (Fig. 76) show a great variety of such centrifugally developed protuberances, in the form of points, ridges, reticulations, and bands of an often complicated internal structure.

Cell-wall Substance (29).—The most important constituent of cell walls is CELLULOSE. With the exception of the Fungi it is present in the cell walls of all plants.

Cellulose is a carbohydrate of which the chemical composition is expressed by the general formula $(C_6H_{10}O_5)n$. It is insoluble in either dilute acids or alkalies. By the action of concentrated sulphuric acid it is converted into dextrose. After treatment with sulphuric or phosphoric acid, iodine will colour it blue; it shows a similar reaction when exposed to the simultaneous action of a concentrated solution of certain salts, such as zinc chloride or aluminium chloride, and of iodine. Accordingly, chloroiodide of zinc, on account of the blue colour imparted by it, is one of the most convenient tests for cellulose. GILSON (30) obtained cellulose in a crystalline condition in the form of sphærites or dendrites.

The cell walls never consist entirely of pure cellulose, but contain a considerable amount of other substances, which are not stained blue by chloroiodide of zinc. In unlignified cell walls PECTOSE is particularly prominent. It is easily distinguished by the readiness with which it dissolves in alkalies, after being previously acted upon by a dilute acid.

Susceptibility to certain stains, for example congo red, is a characteristic of cellulose; while other stains, such as safranin and methylene blue, colour pectose more deeply. According to MANGIN (29), the partition wall formed in the higher plants during cell division consists almost wholly of pectose; the next developed laminæ, the secondary cell-wall layer, of a mixture of cellulose and pectose; the last formed, or tertiary layer, chiefly of cellulose. If the secondary layer of the cell wall remain unlignified, the amount of pectose contained in it increases with age and helps to strengthen the MIDDLE LAMELLA, or primary cell-wall layer.

Among the substances entering into the composition of cell walls, in addition to cellulose and pectose, mention must be made of CALLOSE. It is characterised by its insolubility in cuprammonia and solubility in soda solution, and in a cold 1 per cent solution of caustic potash. It is coloured a red brown by chloroiodide of zinc, with aniline blue it takes an intense blue, and with corallin (rosolic acid) a brilliant red. Its presence in the higher plants is limited to a few special cases; it envelops the sieve-pits and is always present in calcified cell-wall layers, as, for example, in cystoliths (Fig. 75). Chitin, according to GILSON (31), takes the same place in the cell walls of the Fungi as cellulose in the cell walls of the higher plants.

Where cell walls become LIGNIFIED or SUBERISED, it is particularly the secondary layer that receives the wood or cork substance, while the tertiary or internal layer retains its cellulose character.

Lignification depends on the introduction into the membrane of certain substances, among which, according to CZAPEK (32), an aromatic aldehyde which he names hadromal is never wanting. Associated with this is coniferin, which can be obtained from the youngest xylem. CZAPEK denies the existence of vanillin in lignified membranes. The proportion in which hadromal is found in wood does not exceed 1-2 per cent of its dry weight. To its presence the so-called lignin reactions are due, a violet coloration with phloroglucin and hydrochloric acid, and a yellow coloration with acid anilin sulphate. With chlor-zinc-iodide lignified membranes stain yellow, not blue.

Suberised cell walls take a yellowish brown colour with chloroiodide of zinc; with caustic potash, a yellow. VAN WISSELINGH (33) has disputed the presence of cellulose in suberised cell walls, and regards the cork substance or SUBERIN as a fatty body, which is composed of glycerine esters and other compound esters, as well as of one or more other substances which are infusible, insoluble in chloroform, and decomposed by a solution of caustic potash.

CUTINISATION, which is similar to but not identical with suberisation, is usually due to the subsequent deposition of cutin in cellulose cell walls.

VAN WISSELINGH has shown that phellonic acid, which is always present in suberin, is constantly absent in cutin. Cutin withstands better the action of caustic potash. In other respects, the reactions given by cutinised cell walls with chloroiodide of zinc or solutions of caustic potash are almost identical with those of suberised cell walls.

Young cell walls are less elastic, but relatively more extensible than older ones. The power of resisting a stress is increased by lignification. The presence of cutinised and corky membranes at the surface of the plant diminishes the loss of water from it (34).

The layers of the cell walls of some cells, particularly the superficial cells of certain fruits, as of Sage, and of numerous seeds, such as Flax and Quince seeds, become mucilaginous, and swell in water to a slime or vegetable mucus, which, according to G. KLEBS (35), serves the purpose of attaching the seeds to the soil. Firm cell walls can also be transformed into GUM, as is so often apparent in Cherry and Acacia trees, portions of whose woody cells often succumb to GUMMOSIS.

The several varieties of gums and vegetable mucus react differently, according as they are derived from cellulose, callose, pectose, or from allied substances. According to MANGIN they may be microchemically distinguished by their reaction with ruthenium red, which stains only such as are derived from pectose or related substances, such as the mucilage of the seeds of the *Cruciferae* and Quince (*Cydonia*), the mucus cells of the *Malveae*, the gums of the Cherry and Acacia, the gum tragacanth from *Astragalus gummifer*. The mucus of Orchid tubers, on the other hand, is related to cellulose, and remains uncoloured with the same reagent.

The cell walls of the seeds of many Palms, as also those of *Ornithogalum* (Fig. 71), have strongly developed thickening layers, which are full of pits. These thickening layers are lustrous white, and, as in the case of the seeds of the Palm, *Phytelephas macrocarpa*, may attain such a degree of hardness as to be technically valuable as vegetable ivory. Such thickening layers may contain other carbohydrates in addition to cellulose; thus the cell walls of the seeds of *Tropaeolum* and *Paeonia* contain AMYLOID, which turns blue even with iodine alone. These thickening layers are dissolved during germination, and are accordingly to be considered as a reserve substance of the seeds.

Cell walls often become coloured by tannin or derivative substances; in this way, for instance, the dark colour is produced which is often seen in the shells of seeds and in old wood. The colours of the woods of economic value are due to such discoloured cell walls. Inorganic substances are often deposited in large quantities in old cell walls. Among such substances calcium oxalate is often met with, commonly in crystal form; also calcium carbonate, although perhaps not so frequently. In the cystoliths of *Ficus elastica* (Fig. 75) so much calcium carbonate is deposited that it effervesces with hydrochloric acid. In many plants, as, for instance, most of the *Characeae*, the quantity of calcium carbonate in their cell walls is so great as to render them stiff and brittle. Silica is also present in the superficial cell walls of the *Gramineae*, *Equisetaceae*, and many other plants.

Cell Forms.—As cytoplasm is a viscous fluid, and would tend, if unimpeded, to take a spherical shape, it may be assumed that the natural and primary form for cells is spherical. Such a shape, however, could only be realised by cells which, in their living condition, were completely free and unconfined, or in such as were able to expand freely in all directions. Newly-developed cells, which are in intimate union, are, at first, always polygonal. Through subsequent growth their shape may change. The cubical cells of the growing point either elongate to a prism or remain short and tabular. If the growth is limited to certain definite points, and is regular, they become stellate; if irregular, their outline is correspondingly unsymmetrical. In consequence of energetic growth in length, fibre-like, pointed cells are developed. If the walls of such cells become much thickened, they are called SCLERENCHYMA fibres (Fig. 77, *A*). These show diagonal markings, due to their elongated pits, which are generally but few in number. When fully developed, the living contents of such cells are small in amount and frequently they contain only air. In the last case, they merely act as mechanical supports for the other parts of the plant. Cells somewhat similar, but shorter and considerably wider, not sharpened at the ends, and provided with bordered pits, are called TRACHEIDS (Fig. 77, *B*). The tracheids, in their fully developed condition, never have any living contents, but serve as water-carriers for the plant. So long as they remain active, they contain only water and isolated air-bubbles;

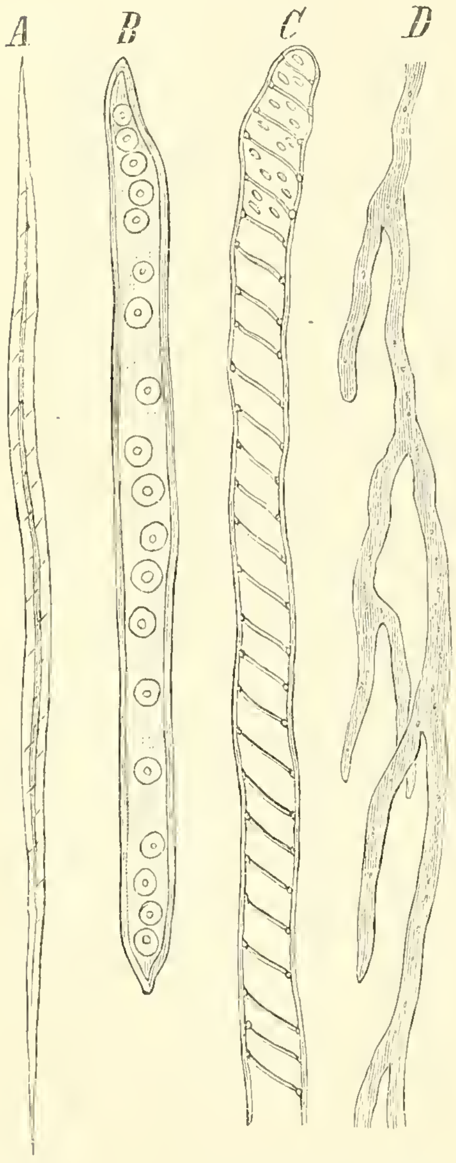


FIG. 77.—*A*, A sclerenchymatous fibre; *B*, a tracheid; *C*, part of a spiral tracheid; *D*, part of a latex tube. (*A*, *B*, *C* × 100; *D*, × circa 150.)

their active functions afterwards cease, and they become filled with air. Tracheids which are specially elongated, and at the same time have only a narrow lumen, and, like the sclerenchymatous fibres, serve merely mechanical purposes, are known as FIBRE TRACHEIDS. Very long tracheids with a wide lumen and thin walls, functioning, like typical tracheids, as water-carriers, are distinguished as vasiform or VASCULAR TRACHEIDS (Fig. 77, *C*). They are characterised by the annular, spiral, or reticulate markings of their thickening layers, and may also be provided with bordered pits. The walls of tracheids are always lignified, while those of the sclerenchyma fibres may or may not have undergone this change.

Of all the cells in the more highly organised plants, the LATEX CELLS or milk cells, also spoken of as latex tubes, attain the greatest length. In the *Euphorbiaceae*, *Urticaceae*, *Apocyneae*, and *Asclepiadaceae* they arise from cells which are already differentiated in the embryo. Growing as the embryo grows, they branch with it and penetrate all its members, and may thus ultimately become many metres long. The latex cells themselves have, for the most part, unthickened smooth elastic walls which give a cellulose reaction. They are provided with a peripheral layer of living cytoplasm and numerous nuclei. Their sap is a milky, usually white fluid, which contains gum-resins, *i.e.* a mixture of gums and resins, caoutchouc, fat and wax in emulsion. In addition, they sometimes hold in solution gums, tannins, often poisonous alkaloids, and salts, especially calcium malate, also in the case of *Ficus Carica* and *Carica Papaya*, peptonising ferments. In the latex cells of the *Euphorbiaceae* there are also present in the latex peculiar dumb-bell shaped starch grains. On exposure to the air the milky sap quickly coagulates. In the adjoining figure (Fig. 77, *D*) is shown a portion of an isolated latex cell dissected out of the stem of an Asclepiadaceous plant, *Ceropegia stapelioides*.

Special cells, which differ in form, contents, or in their peculiar wall thickenings from their neighbouring cells, are distinguished as IDIOBLASTS. If strongly thickened and lignified, they are called sclerotic cells (stone cells) or sclereids. They often contain ferments; in the *Cruciferae* and some other orders myrosin is thus present, while *Prunus laurocerasus* contains emulsin. In Fig. 84 an idioblast, containing a bundle of raphides, is represented. Idioblasts, resembling tracheids and functioning as water reservoirs, are found between the chlorophyll-containing cells in the leaves of some of the *Orchidaceae*.

Inclusions of the Protoplasm—STARCH.—The chloroplasts in plants exposed to the light almost always contain starch grains. These grains of starch found in the chloroplasts are the first visible products of the assimilation of inorganic matter. They are formed in large numbers, but as they are continually dissolving, always remain small. Large starch grains are found only in the reservoirs of reserve material, where starch is formed from the deposited products of previous assimiliation. Such starch is termed RESERVE STARCH, in contrast to the ASSIMILATION STARCH formed in the chloroplasts. All starch used for economic purposes is reserve starch. The starch grains stored as reserve material in potatoes are comparatively large, attaining an average size of 0·09 mm. As shown in the adjoining figure (Fig. 78), they are plainly stratified. Their stratification is due to the varying densities of the successive layers. They are eccentric in structure, as the organic centre, about which the different layers are laid down, does not correspond with the centre of the grain. The starch grains of the legumes and cereals, on the other hand, are concentric, and the nucleus of their formation is in the centre of the grain. The starch grains of the Bean, *Phaseolus vulgaris* (Fig. 79), have the shape of a flattened sphere or ellipsoid; they show a distinct stratification, and are crossed by fissures radiating from the centre. The disc-shaped starch grains of wheat are of unequal size, and only indistinctly stratified. A comparison of the accompanying figures (Figs. 78, 79), all equally magnified, will give an idea of the varying size of the starch grains of different plants. The size of starch grains varies, in fact, from 0·002 mm. to 0·170 mm. Starch grains 0·170 mm. large, such as those from the rhizome of *Canna*, may be seen even with the naked eye, and have the appearance of brilliant points. In addition to the simple starch grains so far described, half-compound and compound starch grains are often found. Grains of the former kind are made up of two or more individual grains, surrounded by a zone of peripheral layers enveloping them in common. The compound grains consist merely of an aggregate of individual grains unprovided with any common enveloping layers. Both half-compound (Fig. 78, *B*) and compound starch grains (Fig. 78, *C*, *D*) occur in potatoes, together with simple grains. In oats (Fig. 80) and rice all the starch grains are compounds. According to Nägeli (36), the

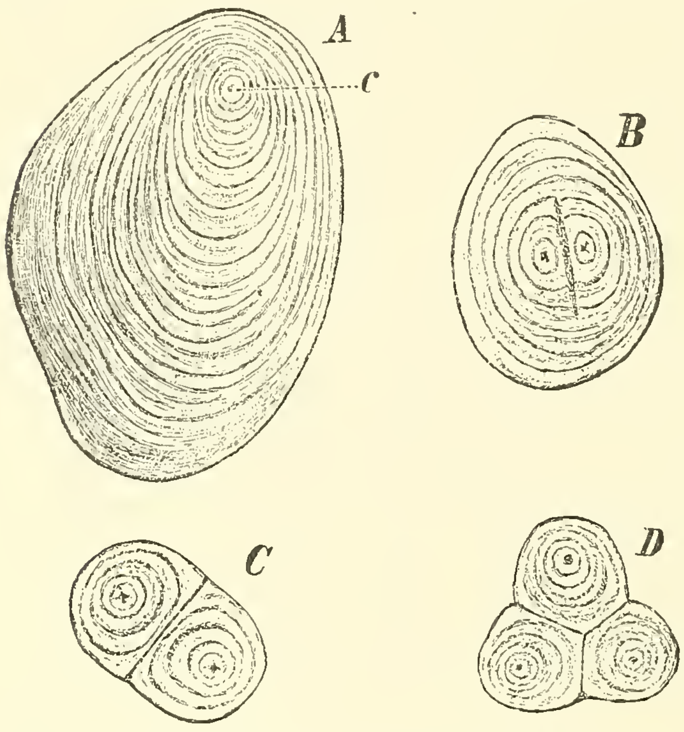


Fig. 78.—Starch grains from a potato. *A*, simple; *B*, half-compound; *C* and *D*, compound starch grains; *c*, organic centre of the starch grains, or nucleus of their formation. (× 540.)

Fig. 79.—Starch grains from the cotyledons of *Phaseolus vulgaris*. (× 540.)

compound starch grains of rice consist of from 4 to 100 single grains; those of *Spinacia glabra* sometimes of over 30,000. Starch thus formed from previously assimilated organic substances also requires chromatophores for its production. It is produced by means of leucoplasts, which are, in consequence, often termed STARCH-BUILDERS. If the formation of a starch grain should begin near the periphery of a leucoplast, the grain would eventually, by its continued enlargement, protrude from the leucoplast. As new layers of starchy matter are then deposited only on the side remaining in contact with the plastid, the starch grain thus becomes eccentric (Fig. 81). Should, however, several starch grains commence to form at the same time in one leucoplast, they would become crowded together and form a compound starch grain, which, if additional starchy layers are laid down, gives rise to a half-compound grain.

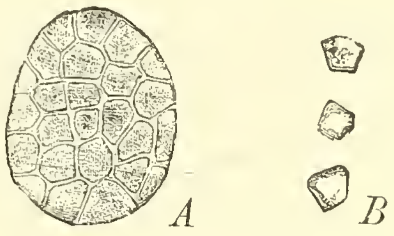


FIG. 80.—Starch grains of oats, *Avena sativa*. *A*, Compound grain; *B*, isolated component grains of a compound grain. (× 540.)

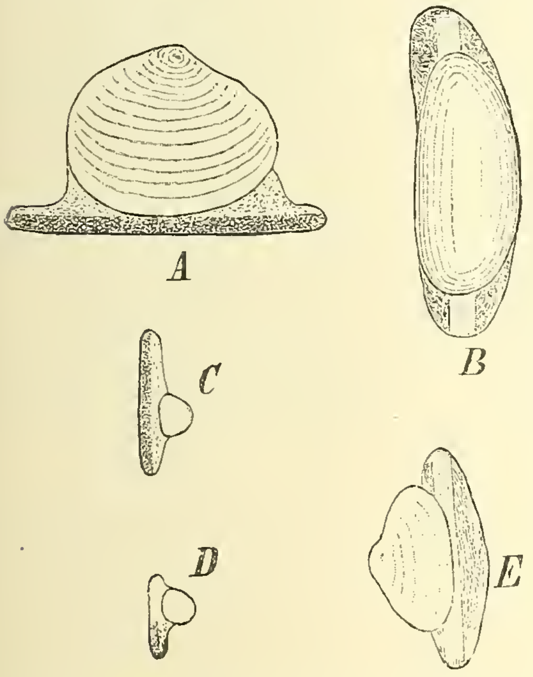


FIG. 81.—Leucoplasts from an aerial tuber of *Phajus grandifolius*. *A*, *C*, *D*, *E*, Viewed from the side; *B*, viewed from above; *E*, leucoplast becoming green and changing to a chloroplast. (× 540.)

It has recently been asserted that starch grains are crystalline bodies, so-called sphærites ([37]), and are composed of fine, radially arranged, needle-shaped crystals, which A. MEYER terms trichites. Their stratification, according to this view, is due to variations in the form and number of the crystal needles in the successive layers. On the other hand, H. FISCHER ([38]) has recently explained the stratification as due to zonal splits rich in water, which originate by contraction taking place in the substance of the grain at some distance from its growing surface. In a few individual cases, ARTHUR MEYER has succeeded in showing that the stratification of the starch grains corresponds to the alternation of the periods of day and night, *i.e.* to the interference which is thus caused in the nutritive processes. The growth of starch grains is also affected by the solvent action of surrounding substances, whereby the peripheral layers may be partially removed, and then no longer completely envelop the entire grain. Starch grains are composed of a carbohydrate, the formula of which is $(C_6H_{10}O_5)n$. Most starch grains only contain amyloid, one variety of which becomes liquid in the presence of water at a temperature of 100° C., and another, which, under the same conditions, does not become liquid. In addition to this amyloid many starch grains contain also amylodextrin. In certain cases, as in *Oryza sativa* var. *glutinosa* and *Sorghum vulgare* var. *glutinosum*, the starch grains consist principally of amylodextrin. Although starch rich in amyloid gives a blue reaction with a solution of iodine, the starch rich in amylodextrin takes a red wine colour. Starch grains becomes swollen in water at a temperature of 60° to 70° C., according to

Arthur Meyer, because of the conversion into tenacious globules of the more readily soluble of the two amyloids; at 138° C. starch grains become completely dissolved. Starch swells very readily at ordinary temperatures in solutions of potassium, or sodium hydrate. Heated without addition of water, *i.e.* roasted, starch becomes transformed into dextrin, and is then soluble in water and correspondingly more digestible. That starch grains give a dark cross in polarised light is due to the double refraction of the component crystalline elements.

The amount of starch contained in reservoirs of reserve material is often considerable; in the case of potatoes 25 per cent of their whole weight is reserve starch, and in wheat the proportion of starch is as high as 70 per cent. The starch flour of economic use is derived by washing out the starch from such reservoirs of reserve starch. In the preparation of ordinary flour, on the contrary, the tissues containing the starch are retained in the process of milling.

Aleurone. — Aleurone or protëin grains are produced in the seeds of numerous plants, especially in those containing oil. They are formed from vacuoles, the contents of which are rich in albumen, and harden into round grains or, sometimes, into irregular bodies of indefinite shape. A portion of the albumen often crystallises, so that frequently one, and occasionally several, crystals are formed within one aleurone grain. In aleurone grains containing albumen crystals there may often be found globular bodies, termed GLOBOIDS, which, according to Pfeffer (39), consist of a double phosphate of magnesium and calcium in combination with some organic substances. Crystals of calcium oxalate are also found enclosed in the aleurone grains.

The seeds of *Ricinus* (Fig. 82) furnish good examples of aleurone grains with enclosed albumen crystals and globoids. The aleurone grains themselves lie embedded in a cytoplasm that is rich in oil. In the cereals the aleurone grains, which lie only in the outer cell layer of the seeds, (Fig. 83, *al*) are small, and free from all inclusions; they contain neither crystals nor globoids. As the outer cells of wheat grains contain only aleurone, and the inner almost exclusively starch, it follows that flour is the richer or poorer in albumen, the more or less completely this outer layer has been removed before the wheat is ground. From the inner layers finer and whiter flour can be made; while more nourishing flour is obtained from the outer layers.

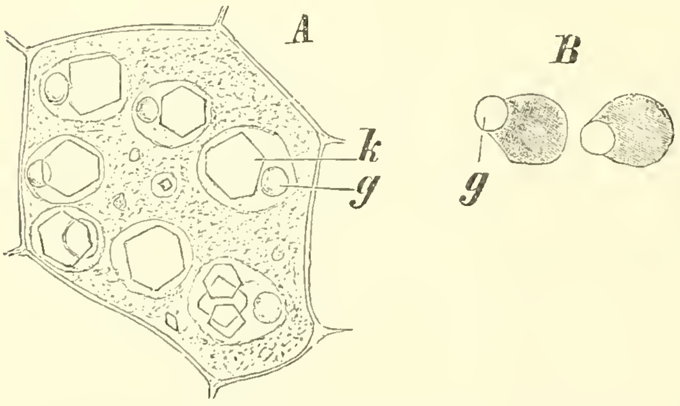


Fig. 82.—*A*, Cell from the endosperm of *Ricinus communis*, in water; *B*, isolated aleurone grains in olive oil; *k*, albumen crystals; *g*, globoid. (× 540.)

Reactions for aleurone are the same as those already mentioned for the albuminous substance of protoplasm. Treatment of a cross-section of a grain of wheat (Fig. 83) with a solution of iodine would give the aleurone layer a yellow-brown colour, while the starch layers would be coloured blue.

Albumen Crystals.—Crystals of this nature are especially frequent in aleurone grains (Fig. 82). They have previously been mentioned as occurring in the chromatophores. In the illustration of the leucoplasts of *Phajus grandifolius* (Fig. 81), the rod-shaped crystals are represented as light stripes (in *B* and *E*). Albumen crystals may also occur directly in the cytoplasm; as, for instance, in the cells poor in starch, in the peripheral layers of potatoes. Albumen crystals are sometimes found even in the cell nucleus. This is particularly the case in the Toothwort (*Lathraea squamaria*), and in many *Scrophulariaceae* and *Oleaceae* (40). Albumen crystals usually belong either to the regular or to the hexagonal crystal system. They differ from other crystals in that, like dead albuminous substances, they may be stained, and also in that they are capable of swelling by imbibition. Subjected to the action of water or a dilute solution of caustic potash, they at first increase in size without losing their crystalline outline.

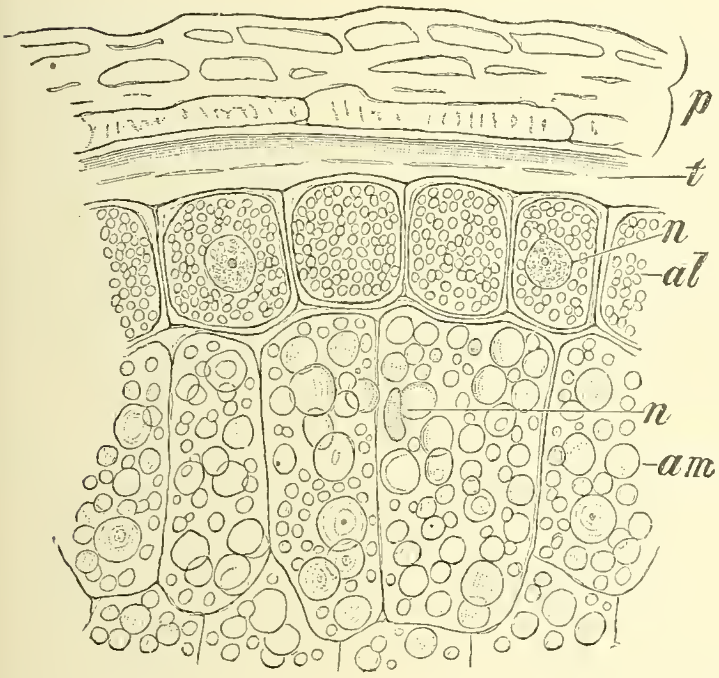


Fig. 83.—Part of a section of a grain of wheat, *Triticum vulgare*. *p*, Pericarp; *t*, seed coat, internal to which is the endosperm; *al*, aleurone grains; *am*, starch grains; *n*, cell nucleus. (× 240.)

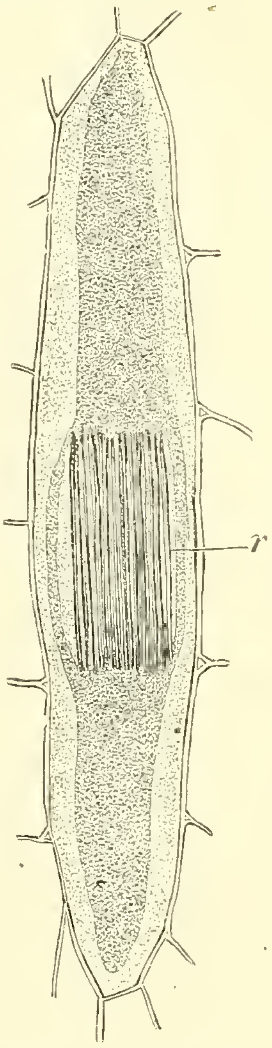


Fig. 84.—Cell from the cortex of *Dracaena rubra*, filled with mucilaginous matter and containing a bundle of raphides, *r*. (× 160.)

Crystals of Calcium Oxalate.—Few plants are devoid of such crystals. They are formed in the cytoplasm, within vacuoles which afterwards enlarge and sometimes almost fill the whole cell. In such cases the other components of the cell become greatly reduced; the cell walls at the same time are often converted into cork, and the whole cell becomes merely a repository for the crystal. The crystals may be developed singly in a cell, in which case they belong either to the tetragonal or monosymmetrical crystal system; or, as is more frequently the case, they form CRYSTAL AGGREGATES, clusters of crystals radiating in all directions from a common centre. In the *Liliaceae*, *Orchidaceae*, and other Monocotyledons, compact bundles of needle-shaped crystals of calcium oxalate, the so-called RAPHIDES, are especially frequent (Fig. 84). Such crystal bundles are always enclosed in a large vacuole filled with a mucilaginous substance. The degree of concentration of the mother liquor from which the crystals have separated, determines, according to KNY (41), their crystal form, whether tetragonal or monoclinic.

SILICEOUS BODIES, which are only soluble in hydrofluoric acid, are found in the cytoplasm of many cells, especially of Palms and Orchids, and often completely fill the whole cellular space.

TANNIN.—Highly refractive vacuoles filled with a concentrated solution of tannin are of frequent occurrence in the cytoplasm of cortical cells, and may often grow to a considerable size. The dark-blue or green colour reaction obtained on treatment with a solution of ferric chloride or ferric sulphate, and the reddish-brown precipitate formed with an aqueous solution of potassium bichromate, are usually accepted as tests for the recognition of tannin, although equally applicable for a whole group of similar substances.

FATS and OILS in plants are mixtures of fatty acid esters. Frequently, as in most Monocotyledons, a fatty oil appears in the old chlorophyll grains. The occurrence of castor oil in the form of highly refractive drops in the cytoplasm of the aleurone-containing cells in the endosperm of the castor-oil seeds, has already been referred to. Oil usually occurs in this form. But fatty substances may also appear in the cytoplasm as irregularly-shaped, more or less soft grains, as for example in the vegetable butters and in the wax of various seeds; they may even be crystalline, as in the needle-like crystals of Para-nuts (*Bertholletia excelsa*) and of Nutmeg (*Myristica fragrans*).

GLYCOGEN.—This substance, related to sugar and starch, and of frequent occurrence in animal tissues, fulfils, according to ERRERA (42), the same functions in the Fungi as sugar and starch in the higher plants. Cytoplasm containing glycogen is coloured a reddish-brown with a solution of iodine. This colour almost wholly disappears if the preparation be warmed, but reappears on cooling.

ETHEREAL OILS AND RESINS.—In most cases the strongly refractive drops found dispersed throughout cytoplasm are globules of some ethereal oil. It is the presence of such oils in the petals of many flowers that gives to them their agreeable perfume. Under certain conditions the oil globules may become crystallised. This occurs, for example, in Rose petals. Secretions from surrounding cells are often deposited in special receptacles in which, through oxidisation, camphor or resin is formed. Special cells of this kind, with corky walls and filled with resin or ethereal oils, are found in the rhizomes of certain plants, as for instance in those of *Calamus* (*Acorus Calamus*) and of Ginger (*Zingiber officinale*); also in the bark, as, for example, of Cinnamon trees (*Cinnamonum*); in the leaves, as in the Sweet Bay (*Laurus nobilis*); in the pericarp and seed of the Pepper (*Piper nigrum*); in the pericarp of Anise seeds (*Illicium anisatum*).

MUCILAGINOUS MATTER is often found as a part of the cell contents in the cells of bulbs, as in *Allium Cepa* and *Urginea Scilla*, in the tubers of Orchids, also in aerial organs, especially in the leaves of Succulents, which, living in dry places, are thus enabled to maintain their water supply by means of their mucilaginous cells.

CAOUTCHOUC AND GUTTA-PERCHA.—These substances are found in a number of plants belonging to different groups, in particular in the *Urticaceae*, *Euphorbiaceae*, and *Sapotaceae*. They occur in the so-called milk sap of special cells in the form of small, dense globules, which, suspended in the watery sap, give it its milky appearance.

LEPTOMIN.—This name was given by RACIBORSKI (43) to a catalytic enzyme, which he found in the sieve-tubes and laticiferous elements of the higher plants, in the milk of the coco-nut, and in the tissues of the potato tuber.

SULPHUR.—As being of unusual occurrence, mention should be made of the presence of sulphur in the form of small refractive grains in the protoplasm of certain Bacteria, the *Beggiatoae*. These Bacteria live in water containing much organic matter, and, according to WINOGRADSKY (44), obtain their sulphur from sulphuretted hydrogen. In fulfilling its function in the Bacteria the sulphur becomes oxidised into sulphuric acid.

The Cell Sap.—Under this term is included especially the fluid which in old cells fills the inner sap cavity. It is generally watery and clearer than the fluid contained in the smaller vacuoles of the cytoplasm. No sharp distinction can, however, be drawn between the sap cavity and vacuoles, and, moreover, a number of such vacuoles may take the place of the sap cavity itself. The cell sap usually gives an acid reaction, owing to the presence in it of organic acids or their salts. The substances held in solution by the cell sap are very various. The soluble carbohydrates, in particular the sugars, cane sugar, the glucoses, and especially grape sugar, frequently occur in the cell sap. The glucoses may be recognised by their reducing properties.

If preparations containing glucose be placed in a solution of copper sulphate, and, after being washed out, are transferred to a solution of caustic potash and heated to boiling, they will give a brick-red precipitate of cuprous oxide. If cane sugar or saccharose be present, this same treatment gives only a blue colour to the cell sap.

Carbohydrates are transported in a plant principally in the form of glucose; cane sugar, on the contrary, is stored up as reserve material; as for example, in the sugar-beet, in the stems of sugar-cane, and in other plants from which the sugar of economic use is derived.

INULIN, a carbohydrate in solution in cell sap, takes the place of starch in the *Compositae*. Treated with alcohol, inulin is precipitated in the form of small granules, which may be redissolved in hot water. When portions of plants containing much inulin, such as the root tubers of *Dahlia variabilis*, are placed in alcohol or dilute glycerine, the inulin crystallises out and forms sphærites, spheroidal bodies composed of radiating crystal needles arranged in concentric layers.

Amides such as GLUTAMIN and ASPARAGIN are also generally present in the cell sap.

There are frequently found dissolved in the cell sap TANNINS, ALKALOIDS, and GLUCOSIDES, such as coniferin, hesperidin, amygdalin, solanin, æsculin, saponin, and also bitter principles related to the glucosides. Organic acids (malic, formic, acetic, and oxalic acids) are also of frequent occurrence in the cell sap; thus, malic acid is usually present in the leaves of the succulents. For the most part, these organic acids unite with bases, and the salts which are formed often crystallise. Of acid salts, which are less frequent than free acids, the binoxalate of potassium found in Field Sorrel (*Rumex*) and Wood Sorrel (*Oxalis*) deserves special mention. Species of *Salicornia* and *Salsola* contain sodium oxalate. The cell sap always contains dissolved inorganic salts, especially nitrates, sulphates, and phosphates.

The cell sap is often coloured, principally by the so-called ANTHOCYANIN. This is blue in an alkaline, and red in an acid reacting cell sap, and, under certain conditions, also dark red, violet, dark blue, and even black. Blood-coloured leaves, such as those of the Purple Beech, owe their characteristic appearance to the united presence of green chlorophyll and anthocyanin. The different colours of flowers are due to the varying colour of the cell sap, to the different distribution of the cells containing the coloured cell sap, and also to the different combinations of dissolved colouring matter with the yellow, yellowish red, or red chromoplasts and the green chloroplasts. There is occasionally found in the cell sap a yellow colouring matter known as xanthein; it is nearly related to xanthophyll, but soluble in water.

2. ONTOGENY OF THE CELL

The Origin of the Living Elements of Protoplasm.—All the nuclei in an organism owe their origin to the nuclei of previous generations. The spontaneous formation of a nucleus never takes place. In the same manner, the cytoplasm of every organism is derived from the cytoplasm of the germ cell, and, so far as is yet known, the chromatophores take their origin only from their own kind.

Nuclear Division.—Except in a few limited cases, nuclei reproduce themselves by MITOTIC or INDIRECT DIVISION. This process, often referred to as KARYOKINESIS, is somewhat complicated, but seems necessary in order to effect an equal division of the substance of the mother nucleus between the two new daughter nuclei.

Indirect Nuclear Division (45).—In its principal features the process is similar in the more highly organised plants and in animals. Its stages are represented in a somewhat diagrammatic manner in the accompanying figure (Fig. 85), as they occur in a vegetative cell such as those which compose the growing point.

The threads composing the clear network of the resting nucleus (Fig. 85, 1) first become thicker and correspondingly shorter, the anastomosing connections forming the meshes are drawn in, while the thread itself straightens out and becomes less entangled, and in consequence more easily distinguished (Fig. 85, 2). At the same time the amount of the chromatin increases, and this increases its capacity of absorbing stains. Finally, the chromatin substance in the thread becomes arranged in parallel discs united by linin. The thread itself then divides transversely into a definite number of segments, the CHROMOSOMES (Fig. 85, 3, 4), which thereupon range themselves in a plane in a special manner, and form the so-called NUCLEAR PLATE (5). Then, or sometimes before, the segments divide longitudinally (6), and the halves thus produced separate from each other in opposite directions (7) to form the daughter nuclei.

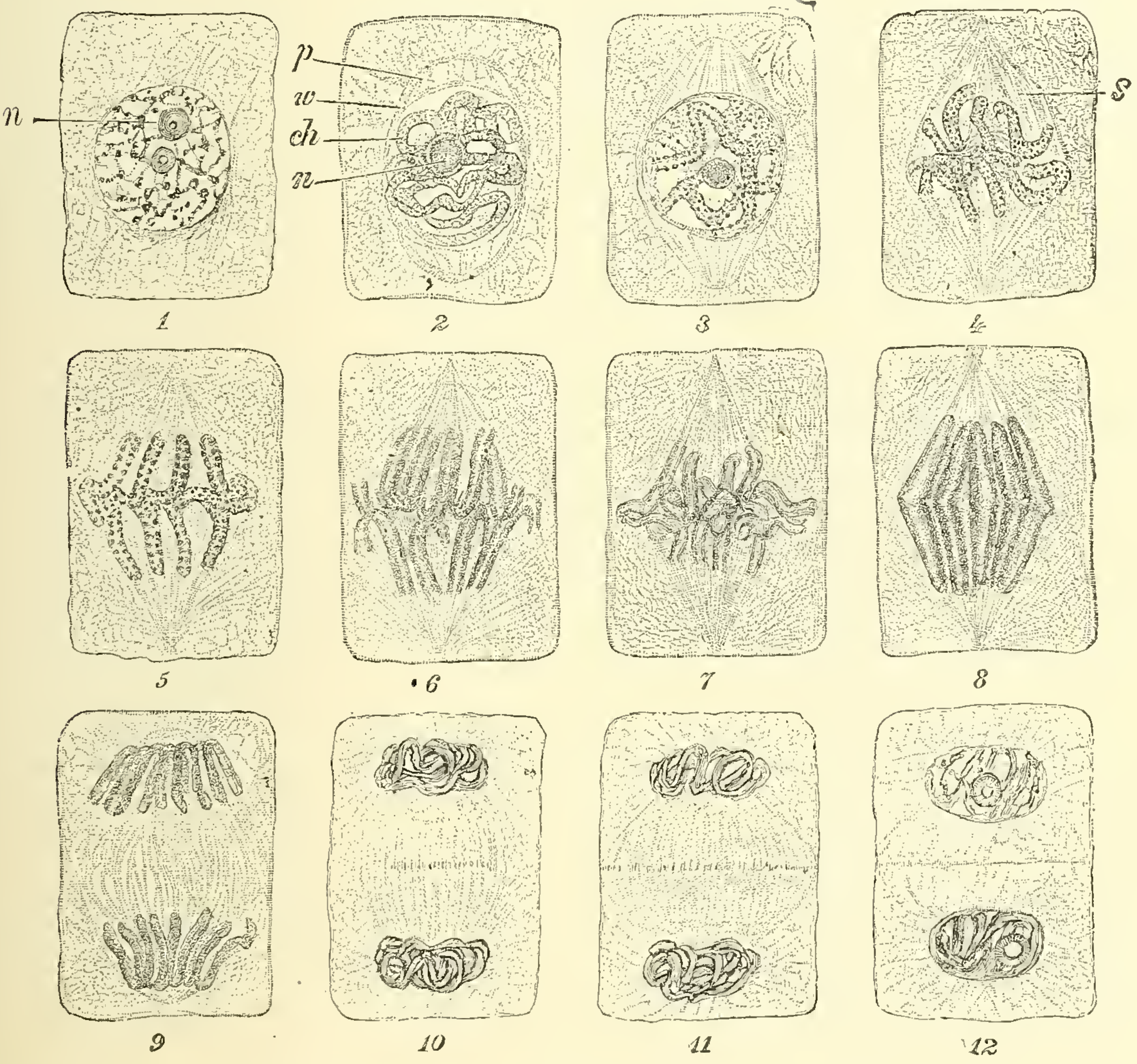


FIG. 85.—Successive stages of nuclear- and cell-division in an embryonic cell such as that of a growing point. Somewhat diagrammatic. *n*, Nucleolus ; *p*, polar caps ; *w*, nuclear membrane ; *ch*, chromosomes ; *s*, spindle fibres. (× about 600.)

Other changes serve to direct the process thus briefly described. While the chromatin-containing filament is becoming shorter and disentangling itself, and then breaking up into the chromosomes, cytoplasmic filaments become applied to the nuclear membrane, surrounding it with a fibrous layer. This layer becomes raised up from the nuclear membrane at two opposite points (2) and forms the polar caps. These are filled with a homogeneous substance in which fine filaments appear later. The latter converge at the poles, without, however, coming into contact; they constitute two pointed bundles, since they diverge from one another as they pass from the polar regions (3). At this stage the nucleoli are dissolved and the nuclear membrane disappears. The fibres proceeding from the polar caps can thus become prolonged into the nuclear cavity (4). Here they either become attached to the chromosomes, or filaments from the two poles may come into contact and extend continuously from the one pole to the other. In this way the nuclear spindle is formed. The fibres of the spindle attached to the chromosomes may be termed traction-fibres, those which run from pole to pole supporting-fibres. In plants the material for the construction of the spindle appears to be mainly derived from the nucleoli. Any excess of nucleolar substance passes into the surrounding cytoplasm, where it forms the so-called extra-nuclear nucleoli. The traction-fibres promote the arrangement of the chromosomes in the equatorial plane (5, 6). After the chromosomes have split longitudinally into the daughter chromosomes, the latter are separated and drawn towards the two poles by the contraction of the traction-fibres (7, 8). The supporting-fibres afford the necessary resistance in the process. The spindle fibres can often be traced to the limiting layer of the cytoplasm, and their attachment to this determined. In forming the daughter nuclei, the free ends of the chromosomes first become drawn in (10), and the surrounding cytoplasm separates itself by means of a protoplasmic membrane (11) from the developing nuclei. Within the nuclear cavities which are thus produced the chromosomes elongate (12), and joining together, end to end, become again intertangled. The chromatin substance is diminished in quantity, nucleoli at length appear in the enlarging nuclei, and finally a condition of rest is again reached.

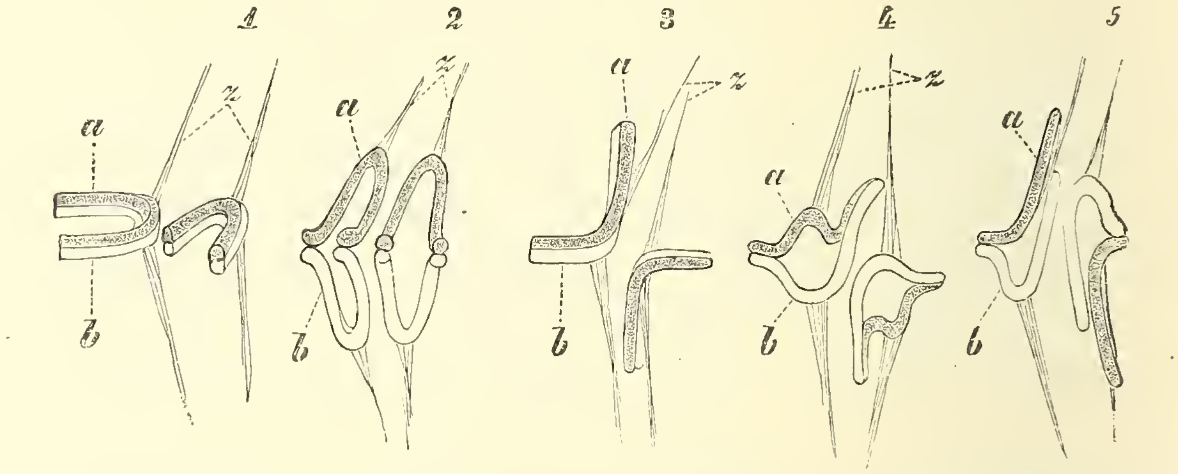


Fig. 86.—Diagrammatic representation of the different positions occupied by the chromosomes in the spindle and during their separation. *a* and *b*, daughter chromosomes of one mother chromosome; *z*, traction-fibres of the spindle.

The process of nuclear division is described above as it usually takes place in the young tissues of more highly organised plants. The chromosomes are usually loop-shaped, and the traction-fibres become attached to the middle point of the loop, less commonly toward an end. The traction fibres from the two poles attach themselves respectively to the two daughter chromosomes of each pair. The orientation of the pairs of daughter chromosomes in the nuclear spindle, and the way in which they separate from one another, is represented in the accompanying diagram (Fig. 86). In (1) the two shanks of each pair of chromosomes lie nearly in the equatorial plane, and each of the daughter chromosomes on their separation (2) assumes the form of the letter U, remaining attached by the shanks. More commonly, while one of the shanks of the paired chromosome lies in the equatorial plane, the other is directed towards one of the two poles (3). In this case a condition of things results, when the daughter chromosomes separate, which is represented in 4 or 5. The former shows the resulting appearance when the daughter chromosomes remain for a time attached to one another at both ends; the latter when separation soon follows at the end directed towards the nuclear pole. In all cases the separation proceeds from the point of attachment of the traction fibres. When a paired chromosome is attached to the spindle near one of its ends, the separation of the daughter chromosomes naturally commences near this end; when the attachment is by the middle of the chromosome the daughter chromosomes remain longer attached by their ends.

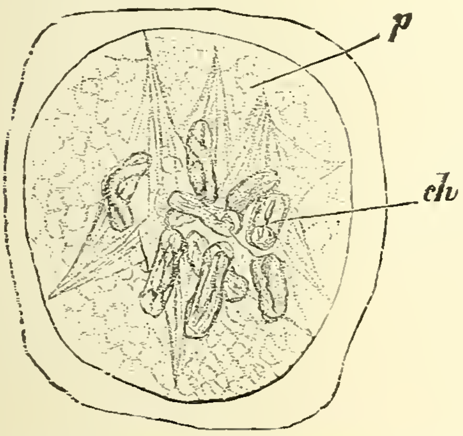


FIG. 87.—Multipolar stage of the spindle in the pollen mother cell of *Lilium Martagon*. *p*, The poles of the preliminary spindle; *ch*, chromosomes. (× 750.)

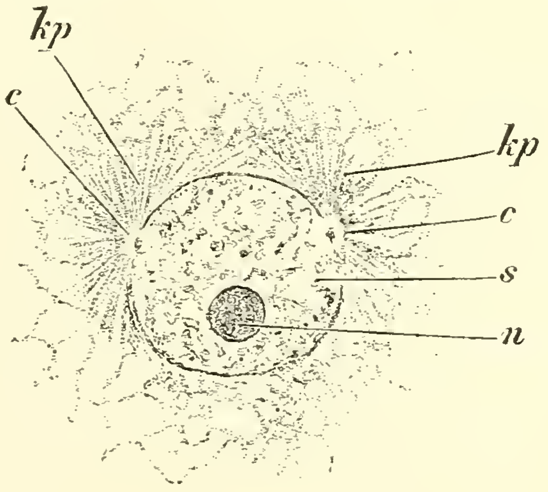


FIG. 88.—A nucleus of a young plant of the Brown Seaweed, *Fucus serratus*, preparing to divide. The two centrosomes (*c*), which have arisen by the division of a single one, have already separated from one another; *kp*, radiations of the fibrillar plasma; *s*, chromosomes; *n*, nucleolus. (× 1000.)

In Fig. 85 the behaviour of the chromosomes is represented as in the diagrams 3 and 4 (Fig. 86). As a rule it does not appear so clearly, but more or less combined with the other type.

In certain reproductive cells of the more highly organised plants the nuclear spindle is not from the first bipolar, as in the vegetative tissues, but is at its appearance multipolar. The bipolar spindle is derived from the multipolar early stage. In Fig. 87 such a multipolar condition of the spindle in a dividing pollen mother cell is represented. Cytoplasmic filaments are differentiated in the alveolar cytoplasm in the neighbourhood of the nucleus, which form at first a network around the latter. From the network single bundles of fibres become separated and extend towards the surface of the cell forming the poles (Fig. 87). The majority of these bundles are later withdrawn, while from those situated at two opposite sides of the nucleus the ultimate poles of the bipolar spindle are derived.

The changes occurring in a mother nucleus preparatory to division are termed the PROPHASES of the karyokinesis. These changes extend to the formation of the nuclear plate, and include also the process of the longitudinal division of the chromosomes. The separation of the daughter chromosomes is accomplished in the METAPHASES, and the formation of the daughter nuclei in the ANAPHASES of the karyokinesis. The real purpose of the whole process is consummated in the quantitative and qualitative division of the chromosomes, resulting from their longitudinal segmentation (6, Fig. 85; *B*, *C*, Fig. 86). The anaphases of the karyokinesis are but a reverse repetition of the prophases.

The nuclear spindle appears to be formed from the constituent of the cytoplasm, which was distinguished above as the fibrillar plasma (p. 58).

In the mother cells of the spores of the higher Cryptogams and of the pollen grains and embryo-sac of the Phanerogams, a reduction in number of the chromosomes occurs on the entry of the nucleus upon the prophase. The reduction is, as a rule, to one half the number present in the nuclei of the surrounding tissues. Two nuclear divisions tend to follow quickly upon this numerical reduction of the chromosomes; the two longitudinal divisions of the chromosomes for these divisions are, however, completed at the commencement of the first division. The appearance of these dividing nuclei differs from what is to be seen in the other tissues. The first of the two divisions has been termed heterotypic, the second homeotypic, while both can be contrasted with the typical division as atypical (46). Corresponding processes of division appear in the preparation of the sexual products of animals.

In those lower Cryptogams, the nuclei of which possess an individualised centrosome, the latter undergoes division into two at the beginning of karyokinesis. The two halves separate from one another (Fig. 88, *c*) and ultimately reach the points which will become the poles of the spindle. Even during the process of separation each centrosome is surrounded by kinoplasmic radiations (*kp*). When the centrosomes have reached the poles the nuclear membrane disappears, and spindle fibres appear in the nuclear cavity itself. These clearly proceed from the centrosomes and become attached to the chromosomes. The complete nuclear spindle (Fig. 89) has a centrosome with kinoplasmatic radiations (*kp*) at each pole, but in other respects agrees with the spindles of the higher plants, from which centrosomes are absent. The main features of the division and the formation of the daughter nuclei are also similar in the two cases. The centrosomes persist in the daughter nuclei and divide into two on each subsequent nuclear division; the kinoplasmatic radiation around the centrosome is, however, only present during the karyokinetic process (47).

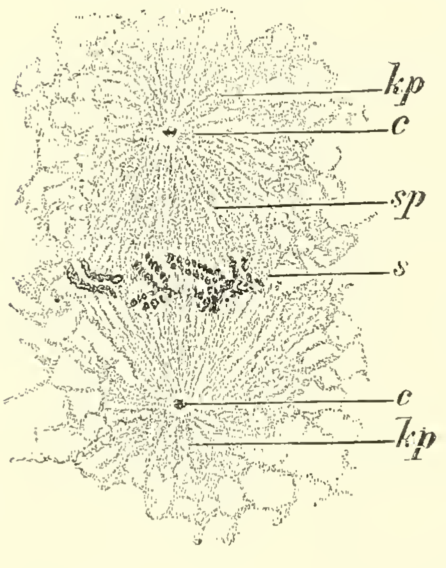


FIG. 89.—A nuclear spindle of a cell of a young plant of the Brown Seaweed (*Fucus serratus*) with split chromosomes in the nuclear plate. *c*, Centrosomes; *kp*, radiations of fibrillar plasma; *sp*, spindle fibres; *s*, longitudinally divided chromosomes forming the nuclear plate. (× 1000.)

Direct Nuclear Division.—In addition to the mitotic or indirect nuclear division there is also a DIRECT or AMITOTIC division, sometimes called FRAGMENTATION (Fig. 90). This may have been the original mode of nuclear division, and among the lowest organisms transitions between it and indirect division are found. In the higher plants direct division of the nucleus is a reduced, or indeed a senile process which usually occurs in old cells, or in cells in which the cell contents become disorganised shortly after the nuclear division.

Instructive examples of direct nuclear division are afforded by the long internodal cells of the Stoneworts (*Characeae*), and also by the old internodal cells of *Tradescantia* (Fig. 90).

The direct nuclear division is chiefly a process of constriction which, however, need not result in new nuclei of equal size. In the case of the Stoneworts, after a remarkable increase in the size of the nucleus, several successive rapid divisions take place, so that a continuous row of bead-like nuclei results. The old internodal cells of *Tradescantia* (Fig. 90) very frequently show half-constricted nuclei of irregular shape. While in uninuclear cells indirect nuclear division is, as a rule, followed by cell division, this is not the case after direct nuclear division.

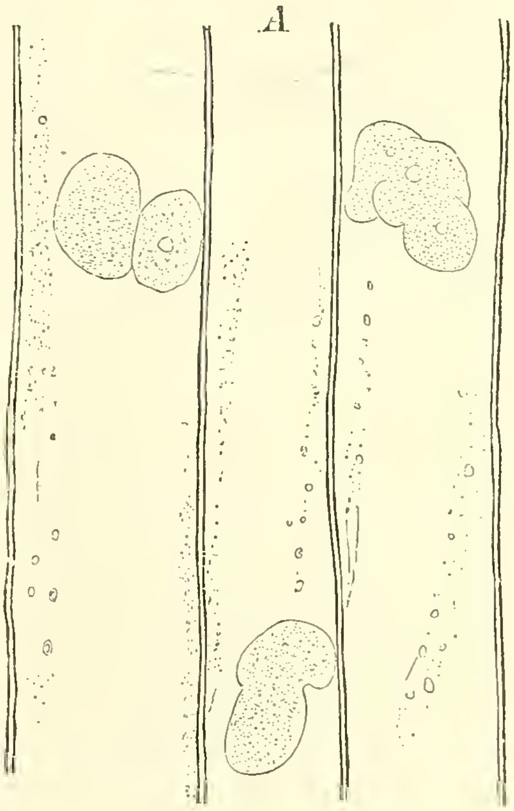


FIG. 90.—Old cells from the stem of *Tradescantia virginica*, showing nuclei in process of direct division. (× 540.)

Cell Division.—In the uninuclear cells of the Cormophytes, cell division and nuclear division are, generally, closely associated as parts of one and the same act. The spindle fibres extending from pole to pole persist as CONNECTING FIBRES between the developing daughter nuclei (Fig. 85, 8, 9). Their number is increased by the interposition of others in the equatorial plane. In consequence of this a barrel-shaped figure is formed, which either separates entirely from the developing daughter nuclei, or remains in connection with them by means of a peripheral sheath, the CONNECTING UTRICLE. The first is the case in cells rich in cytoplasm, the latter when the cells are more abundantly supplied with cell sap. At the same time the connecting fibres become granularly thickened (11) at the equatorial plane, and form what is known as the CELL PLATE. In the case of cells rich in protoplasm or small in diameter, the connecting fibres become more and more extended, and touch the cell wall at all

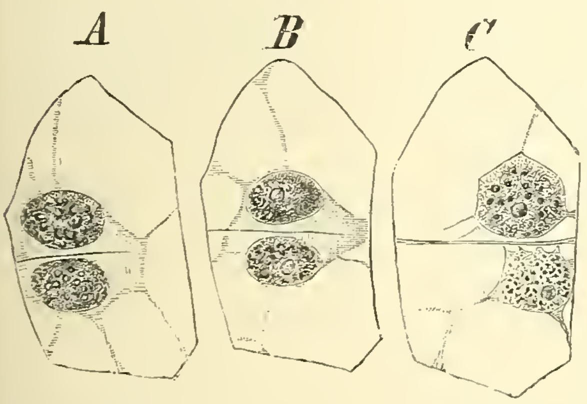


FIG. 91.—Three stages in the division of a living cell of *Epipactis palustris*. (After TREUB, × 365.)

points of the equatorial plane (12). The elements of the cell plate then unite and form a cytoplasmic limiting layer, which then splits into two. In the plane of separation the new partition wall is formed of cell-wall substance, and thus SIMULTANEOUSLY divides the mother cell into two daughter cells (12). If, however, the mother cell has a large sap cavity, the connecting utricle cannot at once become so extended, and the partition wall is then formed SUCCESSIVELY (Fig. 91). In that case, the partition wall first commences to form at the point where the utricle is in contact with the side walls of the mother cell (Fig. 91, *A*). The protoplasm then detaches itself from the part of the new wall in contact with the wall of the mother cell, and moves gradually across until the septum is completed (Fig. 91, *B* and *C*); the new wall is thus built up by successive additions from the protoplasm.

The connecting fibres of the spindle consist of kinoplasm. The origin of the cell plate from swellings of these fibres indicates its kinoplasmatic nature also. By the splitting of the cell plate the limiting layers of the two sister cells are completed across the place of separation. The separation of the complex of connecting fibres into two halves effects an equal division of the kinoplasm between the two new cells.

In the Thallophytes, even in the case of uninuclear cells, the partition wall is not formed within connecting fibres, but arises either simultaneously from a previously formed cytoplasmic plate, or successively, by means of diaphragm-like projections from the wall of the mother cell. It was a division process of this kind (Figs. 92, 93), first investigated in fresh-water Algæ, that gave rise to the conception of cell division, which for a long time prevailed in both animal and vegetable histology. In this form of cell division the new wall commences as a ring-like projection from the inside of the wall of the

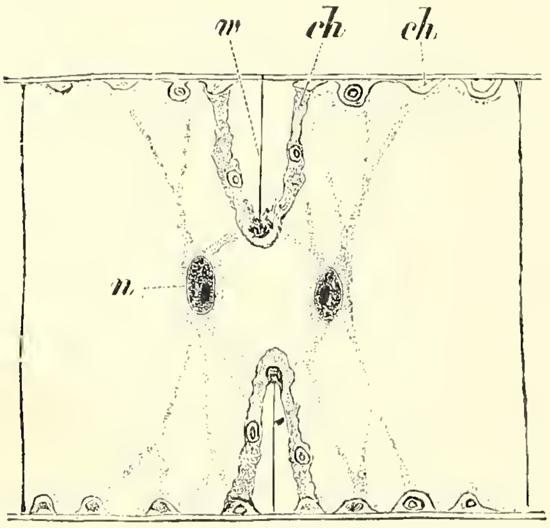


FIG. 92.—Cell of *Spirogyra* in division. *n*, One of the daughter nuclei; *w*, developing partition wall; *ch*, chlorophyll band, pushed inward by the newly-forming wall. (× 230.)

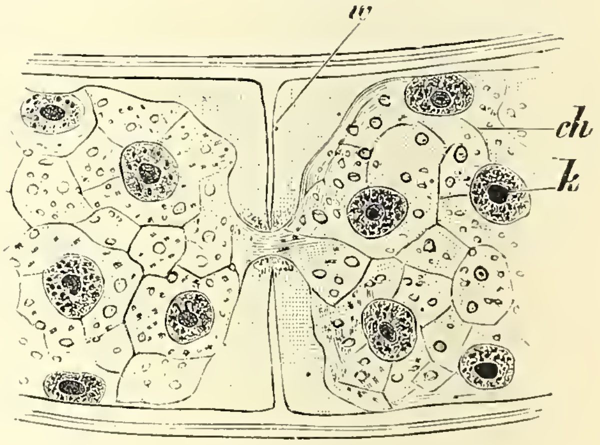


FIG. 93.—Portion of a dividing cell of *Cladophora fracta*. *w*, Newly-forming partition wall; *ch*, intercepted chromatophore; *k*, nuclei. (× 600.)

mother cell, and gradually pushing further into the cell, finally extends completely across it (Figs. 92, 93). In a division of this sort, in uninuclear cells, nuclear division precedes cell division, and the new wall is formed midway between the daughter nuclei (Fig. 92). In the multinuclear cells of the Thallophytes, on the other hand, although the nuclear division does not differ from that of uninuclear cells, cell division (Fig. 93) is altogether independent of nuclear division. And in multinuclear, unicellular Thallophytes, nuclear division is not followed by a cell division. The interdependence of nuclear and cell division in uninuclear cells is necessary to ensure a nucleus to each daughter cell. In multinuclear cells it is not essential that cell division should always be accompanied by nuclear division, as in any case sufficient nuclei will be left to each daughter cell.

Free Nuclear Division and Multicellular Formation.—The nuclear division in the multinuclear cells of the Thallophytes may serve as an example of free nuclear division, that is, of nuclear division unaccompanied by cell division. In plants with typical uninuclear cells, examples of free nuclear division also occur; although, in that case, the nuclear division is customarily followed by cell division. This is often the case in the formation of germ cells, and is due to the fact that while the nuclei increase in number this process is not accompanied by a corresponding cell division. When, however, the number of nuclei is completed, then the cytoplasm between the nuclei divides simultaneously into as many portions as there are nuclei. In this process we have an example of multicellular formation. This method of development is especially instructive in the embryo-sac of Phanerogams, a cell, often of remarkable size and rapid growth, in which the future embryo is developed. The nucleus of the embryo-sac divides, the two daughter nuclei again divide, their successors repeat the process, and so on, until at last thousands of nuclei are often formed. No cell division accompanies these repeated nuclear divisions, but the nuclei lie scattered throughout the peripheral, cytoplasmic lining of the embryo-sac. When the embryo-sac ceases to enlarge, the nuclei surround themselves with connecting strands, which then radiate from them in all directions (Fig. 94). Cell plates make their appearance in these connecting strands, and from them cell walls arise. In this manner the peripheral protoplasm of the embryo-sac

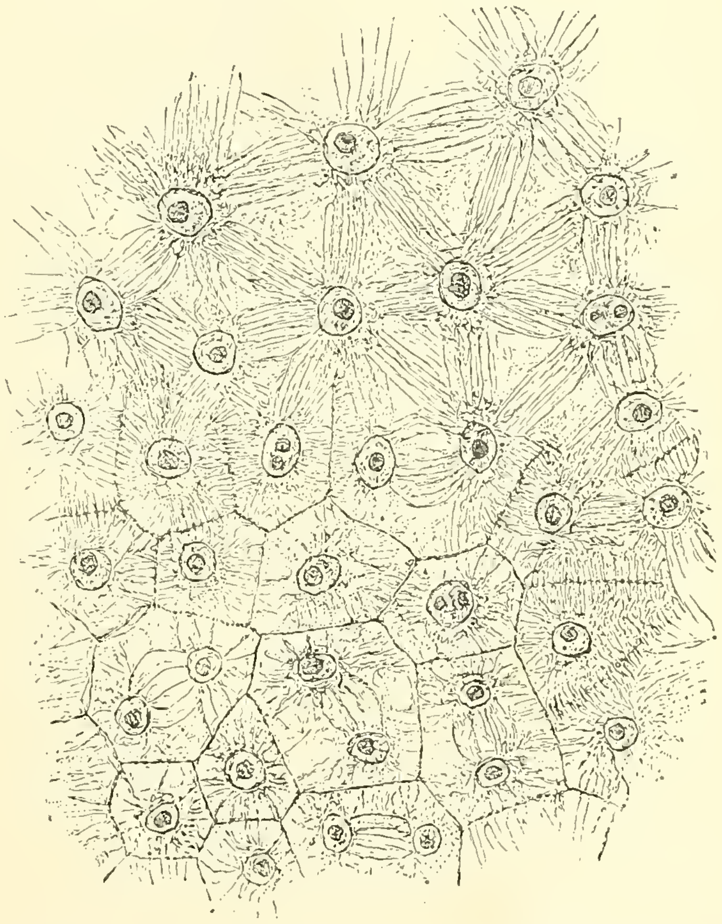


FIG. 94.—Portion of the peripheral protoplasm of the embryo-sac of *Reseda odorata*, showing the commencement of multicellular formation. (× 240.)

divides, simultaneously, into as many cells as there are nuclei. Various intermediate stages between simultaneous, multicellular formation and successive cell division can often be observed in an embryo-sac. Where the embryo-sac is small and of slow growth, successive cell division takes place, so that multicellular formation may be regarded as but an accelerated form of successive cell division, induced by an extremely rapid increase in the size of the sap cavity.

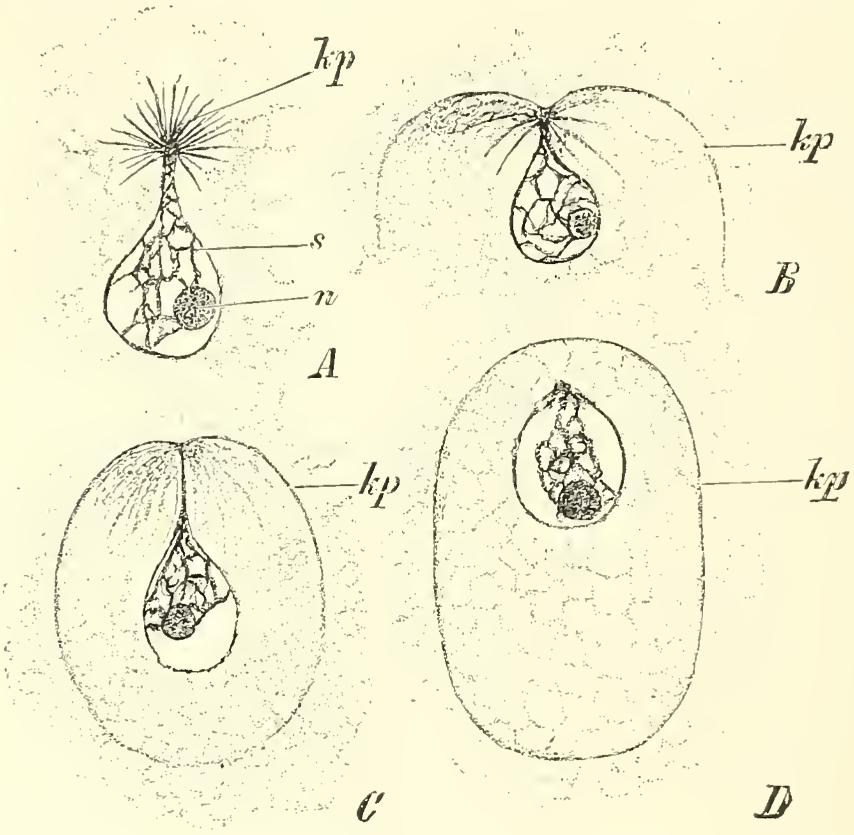


Fig. 95.—Successive stages of the delimitation of a spore in the ascus of *Erysiphe communis*. *A*, Before delimitation has begun; the fibrillar plasma (*kp*) radiates into the cytoplasm around; in *B* the fibrillar plasma has commenced to grow round the mass of cytoplasm; in *C* this process is complete, but the limiting layer produced by the fusion of radiations of the fibrillar plasma is still connected with the polar side of the nucleus; in *D* this kinoplasmatic connection between nucleus and limiting layer has disappeared; *s*, nuclear network; *n*, nucleolus. (After Harper, × 1500.)

Free Cell Formation.—Cells produced by this process differ conspicuously from those formed by the usual mode of cell division, in that the free nuclear division is followed by the formation of cells, which have no contact with each other, and in the formation of which the whole of the cytoplasm of the mother cell is not used up. This process can be seen in the developing embryo of the Gymnosperms, in *Ephedra*, for example, and also in the formation of the spores of the *Ascomycetes*. A single nucleus is present to begin with in each ascus of the Ascomycetes. By successive divisions eight nuclei lying free in the cytoplasm are derived from this. A definite portion of cytoplasm around each of these nuclei becomes limited by a peripheral layer which then forms a cell wall. Thus eight separate spores arise (cf. Fig. 276). As the researches of Harper (48) have shown, the limiting layer of each spore is derived from a mass of kinoplasm aggregated at one side of the nucleus. The radiations of this gradually grow round the mass of cytoplasm (Fig. 95).

Cell-Budding.—This is simply a special variety of ordinary cell division, in which the cell is not divided in the middle, but, instead, pushes out a protuberance which, by constriction, becomes separated from the mother cell. This mode of cell multiplication is characteristic of the Yeast plant (Fig. 2, p. 11); and the spores, known as conidia, which are produced by numerous Fungi, have a similar origin (Fig. 292).

Conjugation (49).—A sexual cell is only able to continue its development after fusion with another sexual cell. The two cells so uniting are either alike, and in that case are called GAMETES, or unlike, and are then distinguished as EGG and SPERMATOZOID. The spermatozoid is the male, the egg the female sexual cell. The gametes may be motile (Fig. 96, *B*) or non-motile. The motile gametes frequently resemble the swarm-spores (Fig. 96, *A*) generated by the same parent for the purpose of asexual reproduction. As a rule, however, they are smaller than the swarm-spores, and have usually only half as many cilia. In the more highly specialised sexual cells the egg usually retains the structure of an embryonic cell, but the spermatozoid undergoes various changes. A cytoplasmic cell body, a nucleus, and

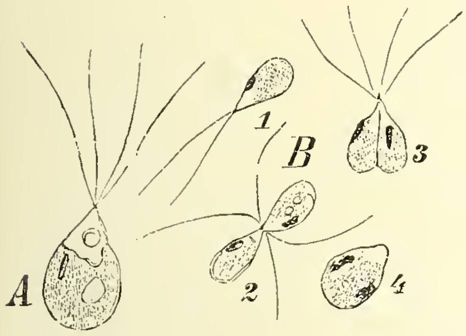


FIG. 96.—*A*, An asexual swarm-spore of *Ulothrix zonata; B*, 1, a gamete; 2 and 3, conjugating gametes; 4, zygote, formed by the fusion of two gametes. (× 500.)

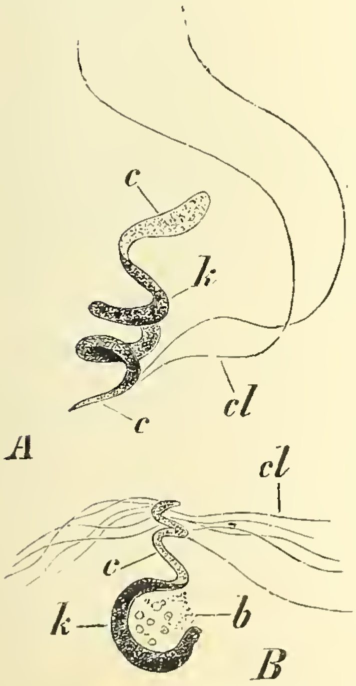


FIG. 97.—*A*, Spermatozoid of *Chara fragilis; B*, spermatozoid of the Fern *Phegopteris Giesbrechtii*. The darker portion, *k*, corresponds to the cell nucleus; the lighter, *c*, to the cell cytoplasm; *cl*, cilia; *b*, vesicle. (× 540.)

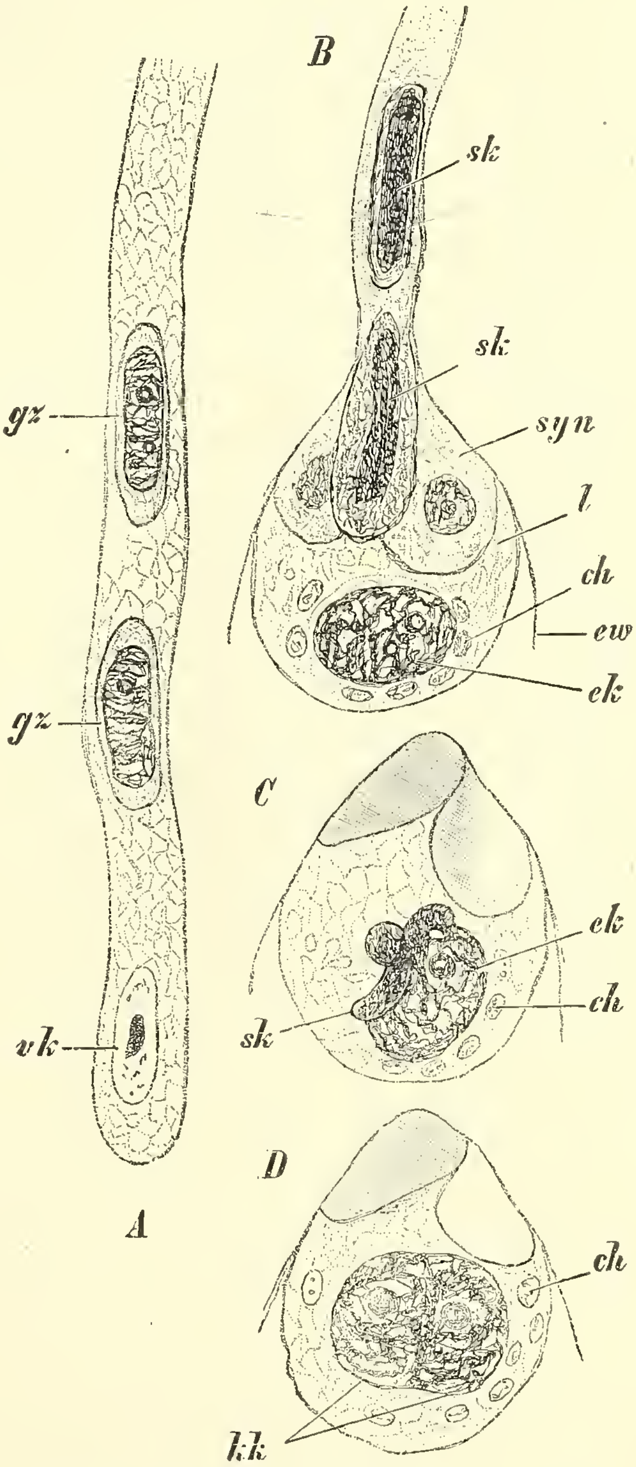


FIG. 98.—Fertilisation of a phanerogamic Angiosperm, somewhat diagrammatic. *A*, End of pollen tube; in it the generative cells *gz*, each of which contains a sperm nucleus; *vk*, the vegetative nucleus in process of dissolution. *B-D*, Egg in successive stages of fertilisation, —*B*, showing the generative cell with its sperm nucleus, *sk*, penetrating the egg; *syn*, the degenerating synergidæ; *C*, the union of sperm nucleus, *sk*, and egg nucleus, *ek*; *D*, the germ nucleus, *kk*, resulting from the fusion of the sperm and egg nuelei; *ch*, rudiments of chromatophores. (× about 500.)

the rudiments of chromatophores are always present in the egg. The male sexual cell (Fig. 97), on the other hand, becomes transformed, in the more extreme cases, into a spirally twisted body, provided with cilia, and exhibiting an apparently homogeneous structure. Only a knowledge of the history of its development, and the greatest care in hardening and staining, have rendered it possible to recognise the homology of the structure of such a spermatozoid with that of an embryonic cell. It has been shown that the hinder part of its spiral body corresponds to the cell nucleus (*k*), the anterior, together with the cilia, to the cytoplasm, especially the kinoplasm (*c*), and the vesicle (*b*), at the other extremity, to the sap cavity of a cell (50).

Motile male cells provided with cilia occur only in the Cryptogams and, as has been recently demonstrated (51), in some Gymnosperms (*Cycadaceae*, *Ginkgo*). In the Cryptogams the spermatozoids are set free from the sexual organs and require water for their dispersal. They reach the egg-cell, which usually remains in its place of origin, by swimming. In the Gymnosperms, which form motile spermatozoids, the latter are brought near to the ovum by means of the pollen tube developed from the pollen grain. In a similar way the non-motile male cells of the other Gymnosperms and the Angiosperms are conducted to the egg through the pollen tube (Fig. 98). In the union of the two sexual cells in the act of fertilisation, the egg nucleus (*ek*) and the sperm nucleus (*sk*) fuse and form the nucleus of the fertilised egg-cell. The cytoplasm of the male cell also commingles with that of the female cell, but the chromatophores of the embryo are derived from the egg-cell alone. When the spermatozoid, as in animals and in Thallophytes, are provided with a centrosome, this does not fuse with the centrosome belonging to the ovum. The centrosome of the fertilised egg-cell appears to be derived from that of the spermatozoid only.

The egg becomes capable of development as the result of fertilisation, although there are exceptional cases in the organic kingdom, especially among the Arthropods, where an unfertilised egg may produce an embryo. This is called PARTHENOGENESIS. In the vegetable kingdom the existence of parthenogenesis in plants with advanced sexual differentiation is extremely rare. For long it was only known in certain Fungi (*Saprolegnieae*) and in *Chara crinita* (52). More recently it has been demonstrated in a Pteridophyte (*Marsilia*) (53), and in the Phanerogams (*Antennaria alpina*, *Achemilla*) (54).

FIG. 99.—Chlorophyll grains from the leaf of *Funaria hygrometrica*, resting, and in process of division. (× 540.)

Multiplication of the Chromatophores.—This is accomplished by a direct division, as a result of which, by a process of constriction, a chromatophore becomes divided into nearly equal halves. The stages of this division may best be observed in the chloroplasts (Fig. 99).

B. Cell Fusions

The connection of the living protoplasts with one another is less complete in plants than in the animal body. This is evident from the existence of the cell wall which surrounds the vegetable protoplast. Recent researches have, however, shown (55) that the protoplasts of the plant are united together by extremely fine cytoplasmic filaments, which proceed from the boundary layer of the cytoplasm. Such filaments are mostly confined to the pit-membrane (Fig. 101), but may also penetrate the whole thickness of the cell wall (Fig. 100). The existence of these connecting filaments of living substance between the protoplasts confers an organic unity on the whole body of the plant.

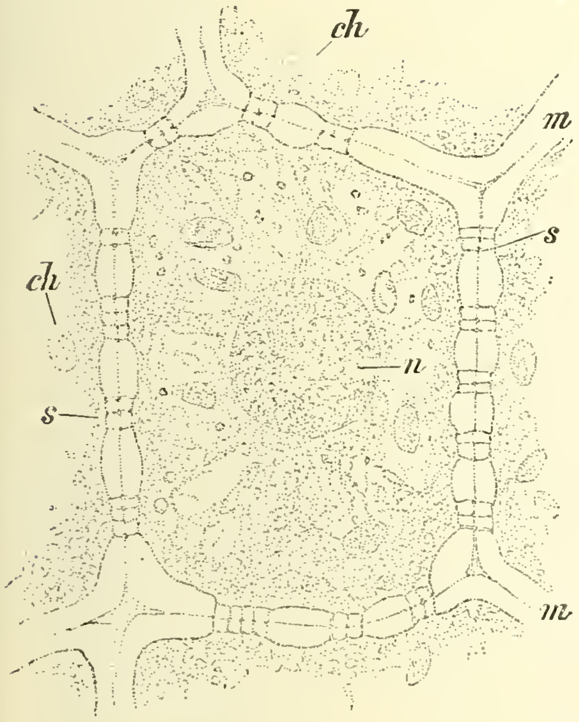


FIG. 100.—A cell from the cortex of the Mistletoe (*Viscum album*); the protoplast has been properly fixed and stained and the wall (*m*) swollen. The pit-membranes (*s*) are traversed by connecting threads; *ch*, chloroplasts; *n*, nucleus. (× 1000.)

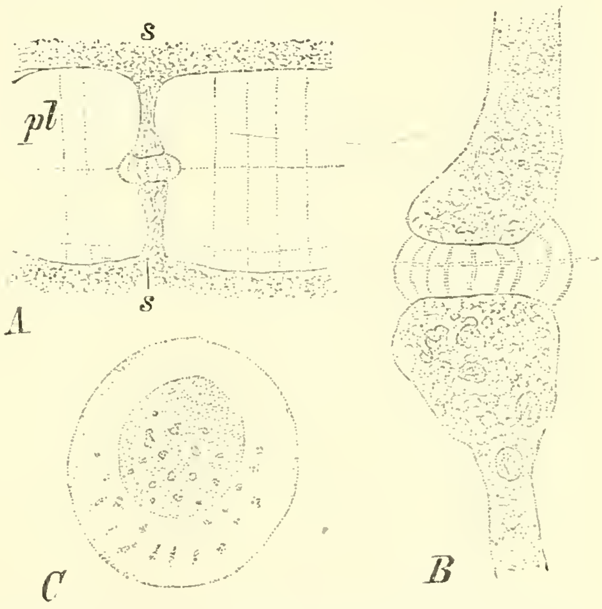


FIG. 101.—*A*, A swollen portion of cell wall from the endosperm of the Vegetable Ivory Palm (*Phytelephas macrocarpa*). At *s*, *s*, simple pits filled with cytoplasm; in the intervening pit-membrane are fine connecting threads; *pl*, other threads traversing the whole thickness of the wall. (× 375.) *B*, The contents of two opposed pits and the connecting threads of the pit-membrane. (× 1500). *C*, The opening of a pit and the connecting threads of the pit-membrane viewed from the surface. (× 1500.)

The members, which make up the sieve-vessels, or, as they are commonly called, the sieve-tubes, are united by thicker strands of cytoplasm, which facilitate the transfer of substances through the tube. The transverse walls traversed by these strands of cytoplasm have been referred to above (p. 67) as sieve-plates. The pores attain their greatest diameter in some Angiosperms (Fig. 102). It is worthy of special note that, despite the fact that the nuclei of the sieve-tube segments disintegrate, the cytoplasm, which lines the wall, remains alive. The walls of sieve-tubes are always unlignified. Their sap-cavities contain a watery, and more or less dilute, solution of albuminous substances, and nearly always small starch grains are also present. As a rule, the sieve-tubes remain functional only through one or a few vegetative periods. Before their activity ceases the sieve-plates become covered (Fig. 102, *C*) with highly refractive callus (p. 68).

A more complete fusion of protoplasts is found in the formation of laticiferous vessels. These have the same structure and contents as latex cells (p. 71). Their occurrence, like that of latex cells, is limited to a few distinct plant families, such as the *Papaveraceae*, of which the Poppy (*Papaver*) or Celandine (*Chelidonium*), with its characteristic orange-coloured "sap," are familiar examples, or the *Compositae*, of which in particular the Lettuce (*Lactuca*) may be cited. Latex vessels are distinguished from latex cells only by the method of their development, which has resulted from the fusion of rows of elongated cells, the separating transverse walls of which have become more or less completely absorbed. Such vessels as a rule possess lateral branches, which, on meeting with one another, fuse by the absorption of their end walls (Fig. 103).

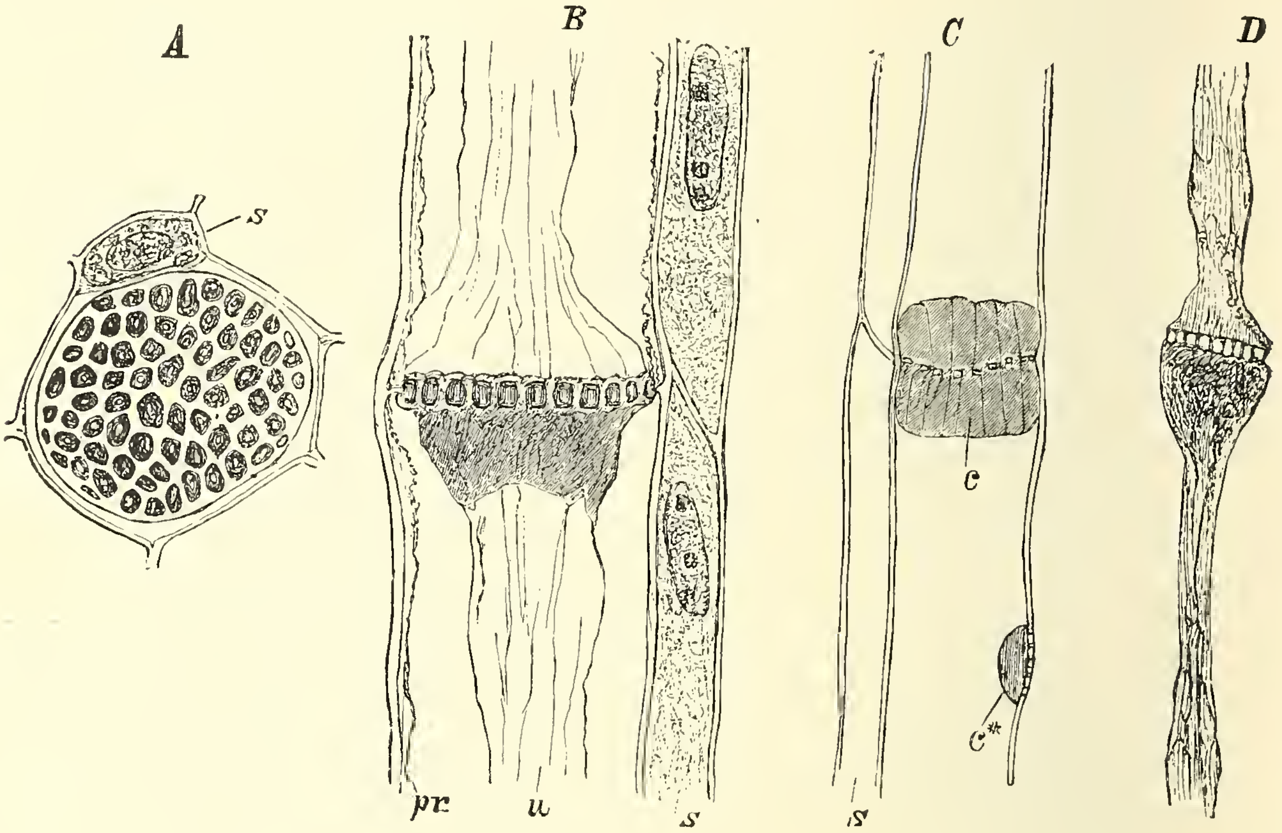


FIG. 102.—Parts of sieve-tubes of *Cucurbita Pepo*, hardened in alcohol. *A*, Surface view of a sieve-plate; *B*, *C*, longitudinal sections, showing segments of sieve-tubes; *D*, contents of two sieve-tube segments, after treatment with sulphuric acid; *s*, companion cells; *u*, albuminous contents; *pr*, peripheral cytoplasm; *c*, callus plate; *c**, small, lateral sieve-pit, with callus plate. (× 540.)

A cell fusion also takes place in the formation of VESSELS or TRACHEÆ, but it should not be considered as a union between living cell bodies, but merely as one between cell cavities. The mature vessels are dead tubes serving for water conduction. They are formed by the absorption of the transverse walls of rows of cells, the lateral walls of which are peculiarly marked by spiral or reticulate thickenings, or, as is more frequently the case, by bordered pits, while the transverse walls become more or less completely absorbed. In cases where the transverse walls are at right angles to the side walls, they usually become perforated by a single round opening while the rest of the wall remains as a thickening ring (Fig. 73, *C*). When the transverse walls are oblique, they are then perforated by several openings, between which portions of the wall remain, like rungs of a ladder (Fig. 104, *q*). According to the mode of their wall thickening, vessels are distinguished as SPIRAL, RETICULATE, or PITTED. When the transversely-elongated pits of a vessel are arranged in more or less parallel rows (Fig. 104), it is called a SCALARIFORM VESSEL. The thickening of the vessel walls is always lignified. The living contents of the cells, after the perforation of the transverse walls, become completely absorbed, and the fully-formed vessels or tracheæ contain only water and a limited amount of air.

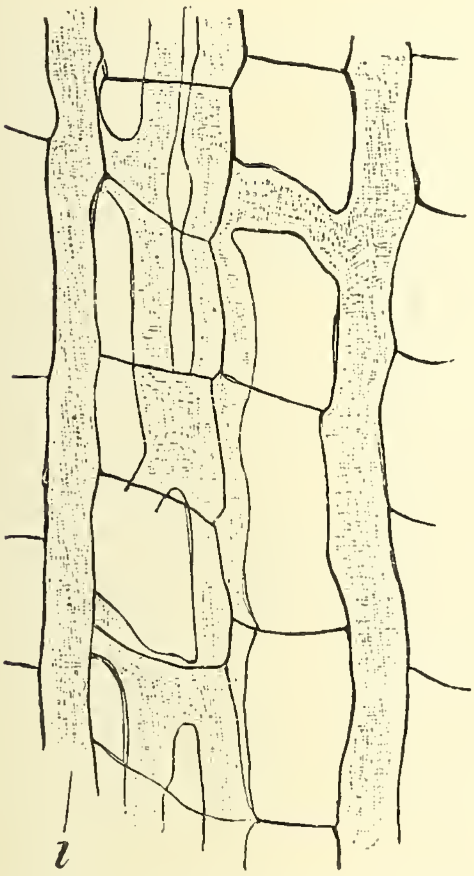


FIG. 103.—Tangential section through the periphery of the stem of *Scorzonera hispanica*, showing reticulately united latex vessels. (× 240.)

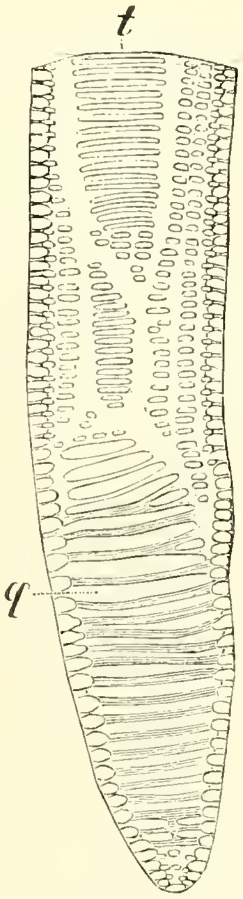


FIG. 104.—Lower third of a scalariform vessel from the rhizome of the common Bracken Fern, *Pteris aquilina*. *t*, Transversely elongated pits in the lateral walls; *q*, scalariform perforations of the terminal wall. (After DE BARY, × 95.)

There is no difference between vasiform tracheids and vessels other than that the former are single elongated cells, and the latter fused cell rows. Generally speaking, tracheids are formed in parts of plants still in process of elongation, vessels in parts where growth in length has already ceased. True vessels make their first appearance in some of the Ferns, for instance, in the common Bracken (*Pteris aquilina*). In the main, despite the name Vascular Cryptogams, Ferns have only vasiform tracheids. Even in the Gymnosperms the *Gnetaceae* are the only family regularly provided with vessels. It is in the Angiosperms that vessels first become of frequent occurrence. Vessels are not of an unlimited length. A few plants, however, such as the Oak, and especially climbing woody plants (Lianes), have vessels several metres long ; but, as a rule, their length is not more than a metre, and in plants, the woody portion of which conducts water only by vessels, the vessels have an average length of only ten centimetres. The length of an individual vessel is defined by the presence of transverse walls, which are not perforated except by bordered pits.

A similar fusion to that seen above to occur in the formation of laticiferous vessels is also met with in fungal hyphæ; by an absorption of a part of the wall where two branches come into contact, their protoplasmic contents unite. A still more complete fusion is exhibited by the naked amœbæ of a myxomycete in forming the plasmodium (p. 55). The fusion of the sexual cells in the process of fertilisation possesses special characteristics which justify its separate consideration.

Tissues (56)

Origin and General Properties of Tissues.—A continuous aggregation of cells in intimate union is called a tissue. The origin of vegetable tissues is, in general, attributable to cell division. It is only in the *Fungi* and *Siphoneae* that a tissue arises through the interweaving of tubular cells or cell filaments (Fig. 105). In such cases, where the filaments are so closely interwoven as to form a compact mass of cells, the apparent tissue thus formed has the same appearance as the tissues of higher plants (Fig. 106).

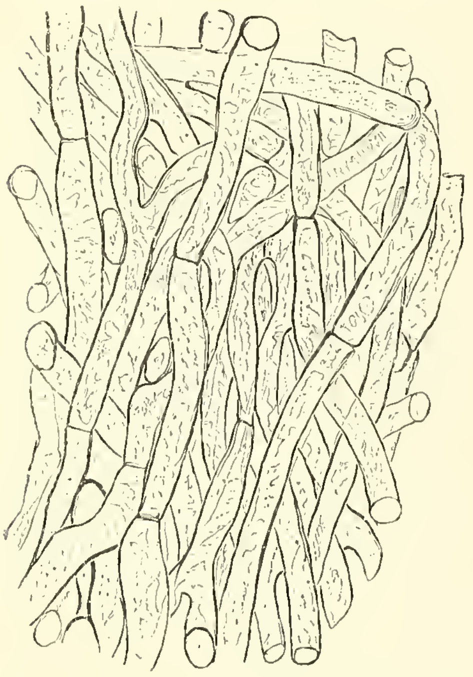


Fig. 105.—Longitudinal section of the stalk of the fructification of *Boletus edulis*. (× 300.)

The mutual interdependence of the cells of a tissue is manifested both by the conjunction of their pits (Figs. 67, 70, 71), and by the general similarity of their wall thickenings.

The cells in a tissue may either fit closely together, leaving no openings or spaces, or so called INTERCELLULAR SPACES may be left between the individual cells. Where cell filaments are interwoven into a tissue, their intercellular spaces are represented by the openings left between the loosely-intertwined filaments (Fig. 105). In tissues resulting from cell division the intercellular spaces arise subsequently, as the partition wall between two cells formed by cell division originally belonged to both mutually.

Such a partition wall may ultimately split and so give rise to intercellular spaces, but this only occurs after it has been thickened. The cause of such splitting is to be found in the hydrostatic pressure existing within the cells, and their consequent tendency to assume a spherical shape. The formation of intercellular spaces commences, therefore, at the cell corners, where the primary wall, consisting of pectinose material, becomes swollen.

The simplest and at the same time most frequent intercellular spaces are triangular or quadrangular in outline, as seen in cross-section (Figs. 67, *i*, 74, *i*). In cases where special portions of adjoining cells are in extremely energetic growth, intercellular chambers and passages, of more or less irregular shape, may be formed between them. If the growth of adjoining cells is very unequal, it may lead to a complete separation of their cell walls; or the cells, or even a whole system of tissues, may be stretched and torn apart. It is by such a process that hollow stems are formed. Intercellular spaces arising from a splitting of adjoining cell walls are accordingly termed SCHIZOGENIC; those formed by tearing or dissolution of the cells themselves are called LYSIGENIC INTERCELLULAR spaces. Most intercellular spaces contain only air, although in special instances they may contain water or excreted products, such as gum, mucilage, resin, or ethereal oils, and in other less frequent cases latex. Schizogenic intercellular spaces are usually filled with air, while the lysigenic spaces contain almost always either water or secretion products.

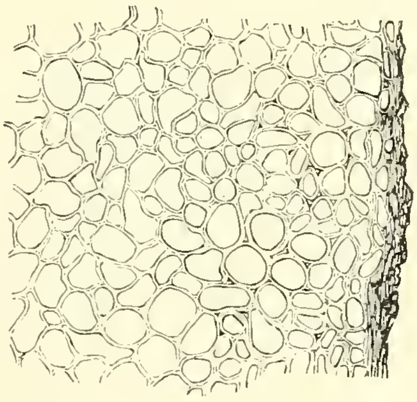


FIG. 106.—Transverse section of the sclerotium of *Claviceps purpurea*. (× 300.)

Of the schizogenic intercellular spaces, those filled with ethereal oils or resin, on account of their frequency, should be particularly noticed. Short cavities and longer passages, or ducts, containing ethereal oils, are to be found in the stems, roots, and leaves of numerous plant families. The *Umbelliferae* are especially rich in these, and the oil-ducts form the characteristic markings (vittæ) on their fruits. The Conifers are especially characterised by resin-ducts (Fig. 140, *h*), which, even during their formation by the separation of the cell walls, seem to fill with an excretion from the cells. The enlargement of such intercellular spaces is accompanied by a division of the surrounding cells, the number of which is thus correspondingly increased. The cells themselves remain thin-walled, and in close contact, but bulge out somewhat into the ducts. Lysigenic intercellular spaces, acting as receptacles for secretions, have the appearance of irregular cavities in the tissue. Where they contain oil or resin, they develop from a group of cells in which these substances appear in the form of drops. The cell group then becomes disorganised by the gradual absorption of the cell walls, beginning with those of the cells in the centre of the group. In this way are formed the receptacles filled with ethereal oils, as, for example, those in *Dictamnus* (*Rutaceae*), and in *Aurantieae*, as in the Orange and Lemon. The exudation of resin, in the case of coniferous trees, is preceded by the formation of abnormal tissues, which afterwards become converted into resin. Such was also the origin of amber, which is the fossil resin of the Amber-fir (*Picea succinifera*). The formation of gum in lysigenic gum cavities is due to the modification of the cell walls, and either normal tissues participate in this process, as in the case of the gum-arabic of the Acacia, or abnormal tissues are first developed and then transformed into gum, as, for example, the gum on Cherry trees. Latex does not occur in lysigenic intercellular spaces.

The separating walls resulting from cell division are simple lamellæ. That part of the partition wall between two cells which stands out so distinctly in a cross-section does not consist of the original primary cell wall alone. It is made up of both the primary wall and the primary thickening layers, and is called the MIDDLE LAMELLA (Figs. 67, *m*, 70, *m*). In soft tissues the middle lamella, according to MANGIN, is composed of pectose combined with calcium (calcium pectate); in woody and corky tissues it has the same composition, but is also lignified. By boiling soft tissues in water, the cells may often be easily isolated through the consequent swelling and dissolution of the middle lamella. In ripe fruits, an isolation of the cells frequently takes place spontaneously, through the dissolution of the middle lamella. A lignified middle lamella, on the other hand, seems able to withstand more effectually the action of oxidising agents. Consequently, it is possible, by subjecting a section of pine-wood to the action of SCHULZE'S MACERATING MIXTURE (potassium chlorate and nitric acid), and subsequently treating with concentrated sulphuric acid, to remove all secondary and tertiary thickening layers, so that only the middle lamellæ remain as a delicate network. If the macerating process be continued for a longer time, without the subsequent treatment with sulphuric acid, the middle lamellæ become finally dissolved. The thickening layer will then be left free from all lignification, and will in that condition give the blue cellulose reaction with chloroiodide of zinc. SCHULZE'S macerating method may accordingly be employed to isolate the elements of lignified tissues. The inexplicable attitude of the middle lamella towards chemical reagents gave rise at one time to the presumption of a peculiar intercellular substance which, like a glue, bound together the cells of a vegetable tissue. The supplementary deposition of pectose in the middle lamellæ (p. 68) frequently gives rise to the formation of rod-like protuberances and excrescences, which project into the intercellular spaces, or these spaces may be filled up by the formation of gussets (Fig. 70, *C*, *m**). The yellowish brown colour assumed by the pectose deposited on the walls of intercellular spaces, on treatment with chloroiodide of zinc, led to the erroneous supposition that the intercellular spaces in plants were lined by a thin layer of living cytoplasm.

Kinds of Tissue.—Vegetable tissues may be divided into two groups, PARENCHYMA and PROSENCHYMA, between which, however, no sharp distinction can be made. A typically developed parenchymatous tissue is one in which the thin-walled cells are equally expanded in all directions, and are, for the most part, rich in protoplasm. Typical prosenchymatous tissue, on the other hand, consists of thick-walled, elongated cells, either in the form of fibres or spindle-shaped cells, with interlocking, pointed ends, and with little or no protoplasmic contents. A parenchymatous tissue, in which the cells are thick-walled and elongated, resembles prosenchyma, but may be distinguished from it by the absence of pointed cell terminations, and especially by the greater abundance of protoplasm. Thin-walled prosenchyma is not, on the other hand, necessarily lacking in protoplasm, but is characterised by its pointed and interlocking cells.

An undifferentiated tissue, the cells of which are still capable of division, is termed embryonic tissue, or MERISTEM. The meristem of embryonic rudiments and of the growing point is called PROMERISTEM, and all meristematic tissue which can be shown to have been developed directly from such promeristem is termed PRIMARY. A primary meristem, in the midst of a completely developed tissue, may still retain its meristematic character. Fully differentiated tissue is designated PERMANENT tissue in contrast to meristematic tissue. At times, permanent tissue may again become capable of division, and in that condition is called SECONDARY MERISTEM.

A mass of tissue so united in the body of a plant as to form a distinct histological unit constitutes a tissue system. In the more highly organised plants three such systems may be distinguished—the TEGUMENTARY SYSTEM, the VASCULAR BUNDLE SYSTEM, and the FUNDAMENTAL TISSUE SYSTEM.

The tissues which make up the different tissue systems are distinguished as PRIMARY and SECONDARY, according as they are derived from the promeristem or secondary meristem.

The PRIMARY TISSUES of the tissue systems will be considered first.

A. The Primary Tissues

The Tegumentary System.—In the Pteridophytes and Phanerogams the plant body is covered by a distinct outer tegument or EPIDERMIS; this is wanting in plants of the lower groups. On the inside, the epidermis, which is usually composed of but a single layer of cells (Fig. 74, *e*), is sharply marked off from the adjoining tissue, while on the outside it is much thickened. This is especially the case in all aerial parts of plants adapted for a long life, but on the more perishable parts of a plant, such as the floral leaves, or on those parts more protected, as the root, the cells of the epidermal layer are generally thin-walled or only slightly thickened. Even when the external walls of the epidermal cells are considerably thickened, the side walls, at least in part, remain unthickened. The external walls are also more or less cuticularised, while their outermost layer, which is more decidedly cuticularised and capable of withstanding even the action of concentrated sulphuric acid, extends as a CUTICLE continuously over the surface of the epidermis. The cuticle has its origin in the primary walls of the younger epidermal cells, which, during the increase in size of the plant, become very much distended, and at the same time strengthened by the deposition of cutin. The cuticle frequently becomes folded, and so assumes a striped appearance (Fig. 113). Plants in dry climates, or so situated that, for any reason, transpiration from their outer surfaces must be diminished, are characterised by the extraordinary thickened and cuticularised walls of their epidermal cells. In some of the *Gramineae*, *Equisetaceae*, and many other plants, the cell walls of the epidermis are silicified. In the *Equisetaceae* the impregnation with silica is so considerable that these plants are used for polishing. Heating, even to redness, does not destroy the structure of such silicified epidermal cells.

Deposits of wax, as DE BARY has shown, are also present in the cutinised layers of the epidermis, and consequently water will flow off the epidermis without wetting it. The wax is sometimes spread over the surface of the cuticle as a wax covering. This is the case in most fruits, where, as is so noticeable on plums, it forms the so-called bloom. The wax coverings may consist of grains, small rods (Fig. 107), or crusts.

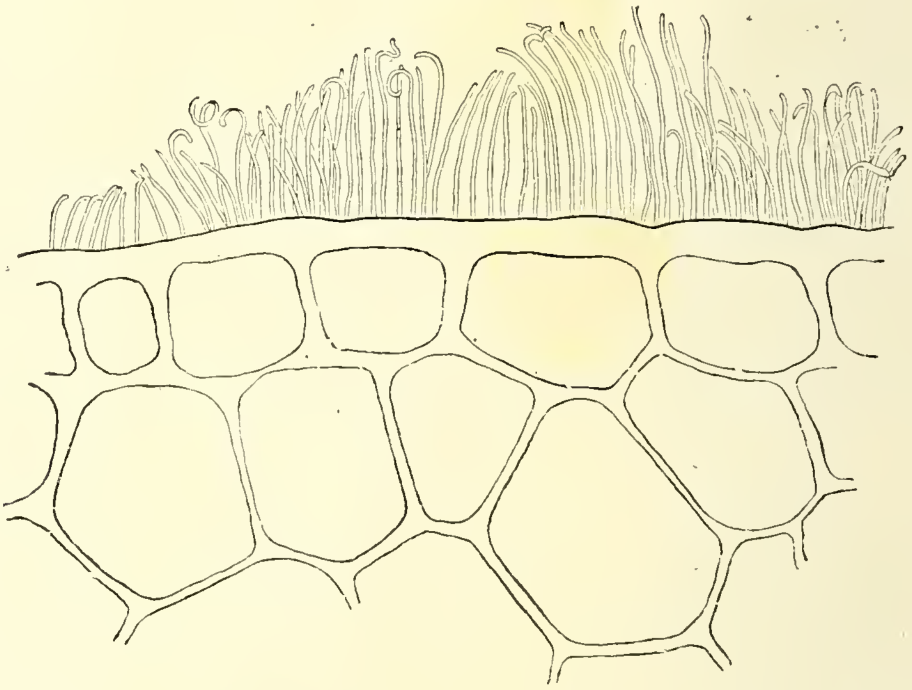


FIG. 107.—Transverse section of a node of the sugar-cane, *Saccharum officinarum*, showing wax incrustation in the form of small rods. (× 540.)

The wax deposits attain their greatest thickness on the leaves of some of the Palms; on the Peruvian Wax Palm, *Ceroxylon andicola*, the wax covering is more than 5 mm. thick. This wax, as well as that obtained from the fruit of *Myrica cerifera*, is known as vegetable wax, and possesses an economic value. The wax incrustations may be melted by heat; they are soluble in ether and in hot alcohol. In many cases, in place of the wax coverings, small grains and scales of a fat-like substance, which is soluble even in cold alcohol, are excreted from the hairy surface of the epidermis. The dusty coverings thus formed appear either mealy white or golden yellow, and are the cause of the striking appearance of the Gold and Silver Ferns, especially in species of *Gymnogramme*.

In many cases, slimy or sticky excretions are produced between the thickening layers of the epidermis and the cuticle, which press up the latter and finally burst it. Such excreting surfaces often occur inside buds. Sticky zones are frequently formed on stems, as in the case of *Lychnis viscaria* and other *Sileneae*, as a means of protection to the buds higher on the stem from undesirable visitors. Small creeping insects, which would otherwise rob the flowers of their honey, seem as little able to pass beyond such a sticky zone, as other larger animals to surmount the rings of tar often placed around the trunks of trees for a similar protective purpose. Excreting epidermal surfaces form also the nectaries of flowers, which by means of their sweet secretions lure such animals, generally insects, as are instrumental in their pollination.

The cells of the epidermis are in uninterrupted contact with each other, and as a rule have undulating side walls (Fig. 108). The protoplasm of epidermal cells generally appears to be reduced to a thin, peripheral layer, and the sap cavities filled with a colourless or coloured sap. Around their nuclei cluster the colourless rudiments of the undeveloped chromatophores, showing that, although exposed to the light, their further development may cease in cells not destined to take part in the assimilatory processes. Such epidermal cells with undeveloped chromatophores, besides acting as an external protection, serve as water-reservoirs; their side walls, by means of folds in the unthickened parts, can expand and collapse as a bellows, according to the variations in their supply of water. In plants which grow in shade chlorophyll is usually present in the epidermal cells (Fig. 109).

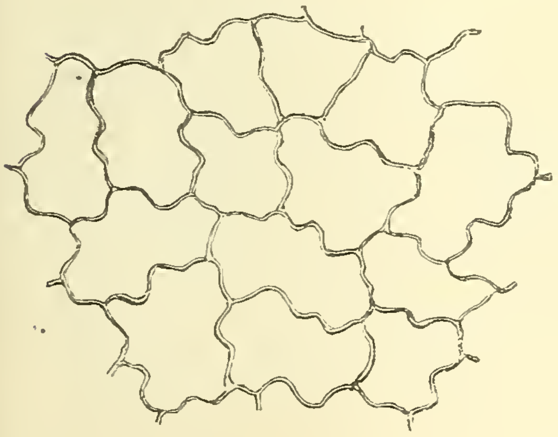


FIG. 108.—Surface view of the epidermis from the upper side of a leaf of *Mercurialis perennis*. (× 300.)

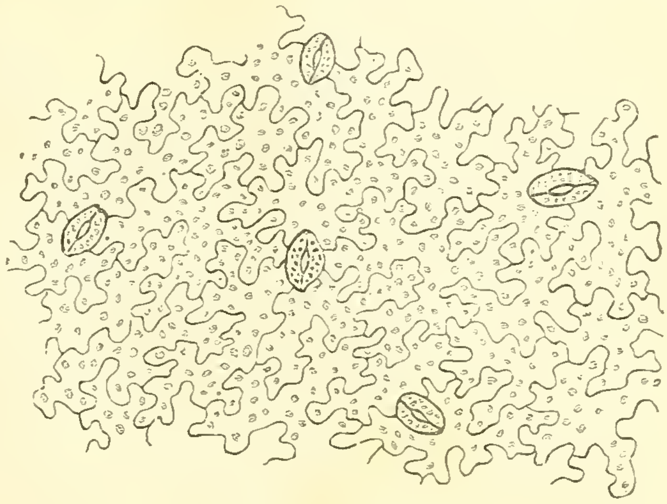


FIG. 109.—Surface view of the epidermis from the under side of a leaf of *Impatiens parviflora*, showing stomata. (× 160.)

The formation of stomata (57) in the epidermis is characteristic of all parts of the more highly-developed plants which are exposed to the air. Each stoma forms an intercellular passage perforating the epidermis and bounded by two elliptical epidermal cells, termed GUARD-CELLS (Fig. 110, *A*). The guard-cells always contain chloroplasts, and are also characterised by their peculiarly thickened walls, which form ridge-like protuberances projecting above and below from the sides of the guard-cells adjoining the air-passage (Fig. 110, *B*).

Midway between the projecting ridges, on the other hand, the walls of the guard-cells remain unthickened (Fig. 111).

The guard-cells themselves jut out into the air-passage (Figs. 110 *B*, 111), and thus facilitate its closing. In addition, the external thickened walls of the two adjacent epidermal cells become, in some cases, suddenly narrowed on approaching the guard-cells. By this means a hinge-like connection is formed which renders the guard-cells independent of the other epidermal cells. At other times the same result is accomplished by raising the stomata above the epidermis, or, which has the same effect, by sinking them below the thickened epidermal walls. Frequently the epidermal cells adjoining the guard-cells are less thickened or lower than the other cells of the epidermis (Fig. 110). Such special epidermal cells are called SUBSIDIARY CELLS.

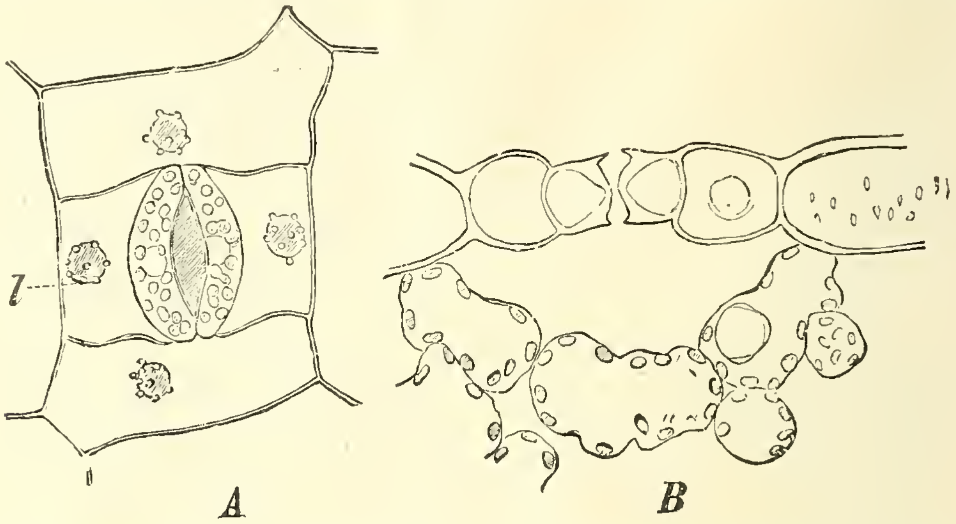


FIG. 110.—Epidermis from the under side of a leaf of *Tradescantia virginica*. *A*, In surface view; *B*, in transverse section; *l*, colourless rudiments of chromatophores surrounding the nucleus. (× 240.)

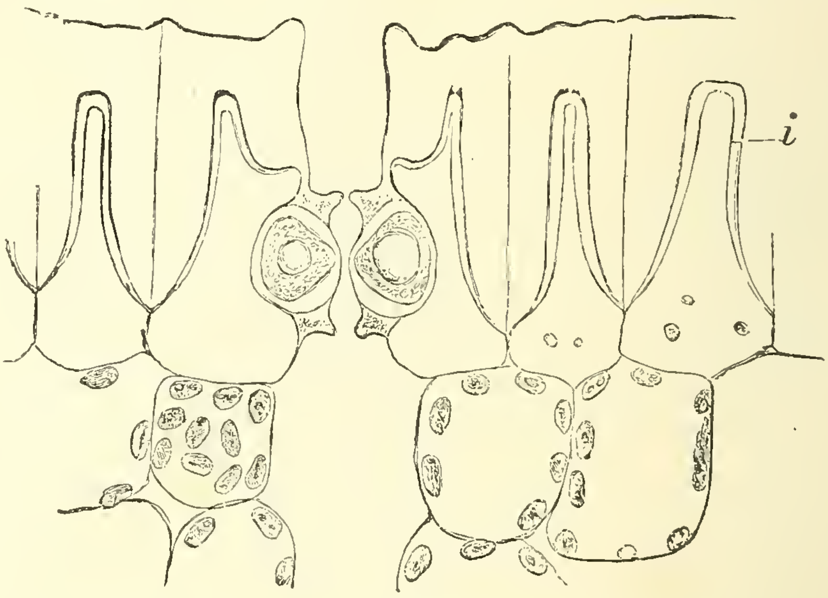


FIG. 111.—Transverse section of the epidermis of *Aloe nigricans*. *i*, Inner, uncutinised thickening layer. (× 240.)

The stomata are formed by the division of a young epidermal cell into two cells of unequal size, one of which, the smaller and more abundantly supplied with protoplasm, becomes the stoma mother-cell; while the larger, containing less protoplasm, usually continues as an epidermal cell. The stoma mother-cell becomes elliptical in outline and divides again, by a vertical wall, into the two guard-cells, between which, by a splitting of the wall, the intercellular passage is formed. Before the formation of the definitive stoma mother-cell, successive divisions of the young epidermal cell often occur; in such cases the finally developed stoma is generally surrounded by subsidiary cells.

Stomata are chiefly developed on the green parts of plants, but are sometimes found even on the coloured floral leaves. They are naturally found in greatest numbers on the leaves, as it is there that they are most needed to facilitate the interchange of gases necessitated by the processes of assimilation. In dorsiventral leaves the stomata occur, for the most part, if not exclusively, on the under surface, and average about 100 to the square millimetre, although in some plants their number may reach 700. Leaves which are alike on both sides have their stomata equally distributed on their upper and under surfaces. Floating leaves of aquatic plants have stomata only on the side exposed to the air. In some cases, as in the Oleander (*Nerium Oleander*), several stomata are situated together in depressions in the under surfaces of the leaves. In the tissue directly under each stoma there is always a large intercellular air-chamber, termed the RESPIRATORY CAVITY (Fig. 110, *B*), which is in direct communication with other intercellular spaces extending throughout the leaf tissue. In plants grown in abundance of moisture, these intercellular spaces in leaves are larger than in the case of plants growing in drier situations.

In contrast to the stomata, which as air-pores serve for the interchange of gases, a few plants also possess WATER-STOMATA or WATER-PORES, situated at the ends of the so-called veins or nerves of the leaves. These pores serve as organs for the discharge of water or watery solutions. Calcium carbonate, in solution, is frequently excreted in this way, and in many species of *Saxifraga* it forms white scales on the margins of the leaves. Although water-pores may often be found at the apices and tips of the marginal teeth of young leaves, they seem to dry up as the leaves become more mature. The guard-cells of water-stomata always lose their living contents prematurely, and thus the passage between them remains continually open. The water-stomata (Fig. 112) are always larger than the

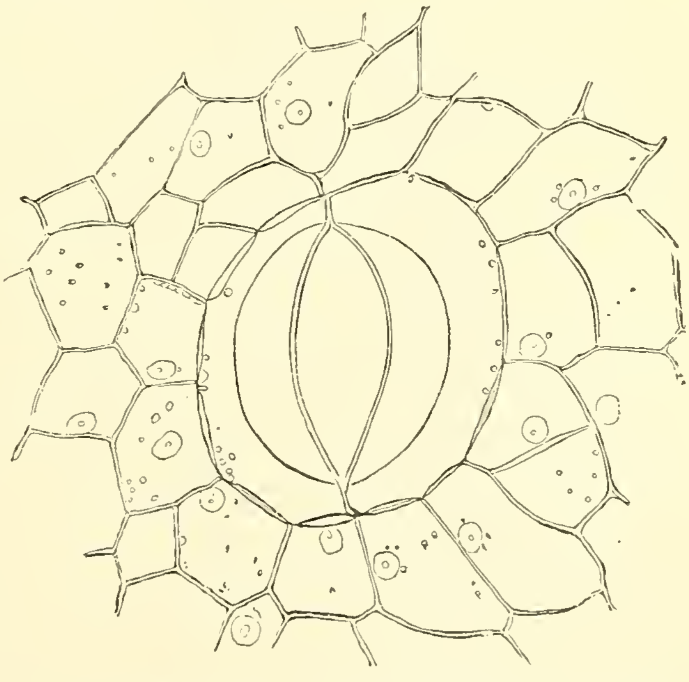


FIG. 112.—Water-pore from the margin of a leaf of *Tropaeolum majus*, with surrounding epidermal cells. (× 240.)

air-stomata. Although submerged leaves of aquatic plants are devoid of air-stomata, water-stomata often occur on them.

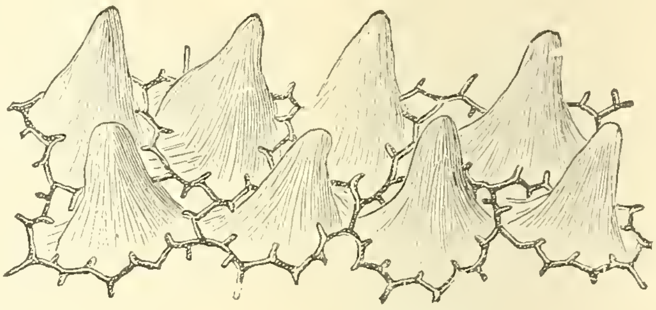


FIG. 113.—Surface of the upper epidermis of a petal of *Viola tricolor*, showing ridge-like projections from the lateral walls, and protruding papillæ. (× 250.)

Hairs or TRICHOMES and tegumentary outgrowths or EMERGENCES are characteristic of the tegumentary system. Their cells may retain their living contents, or die and become filled with air; in the latter case the hairs appear white. The simplest form of hairs are the PAPILLÆ, which are merely epidermal cells, the external walls of which have protruded in a conical form. Papillæ are often developed on the petals of flowers, and are the cause of their velvety

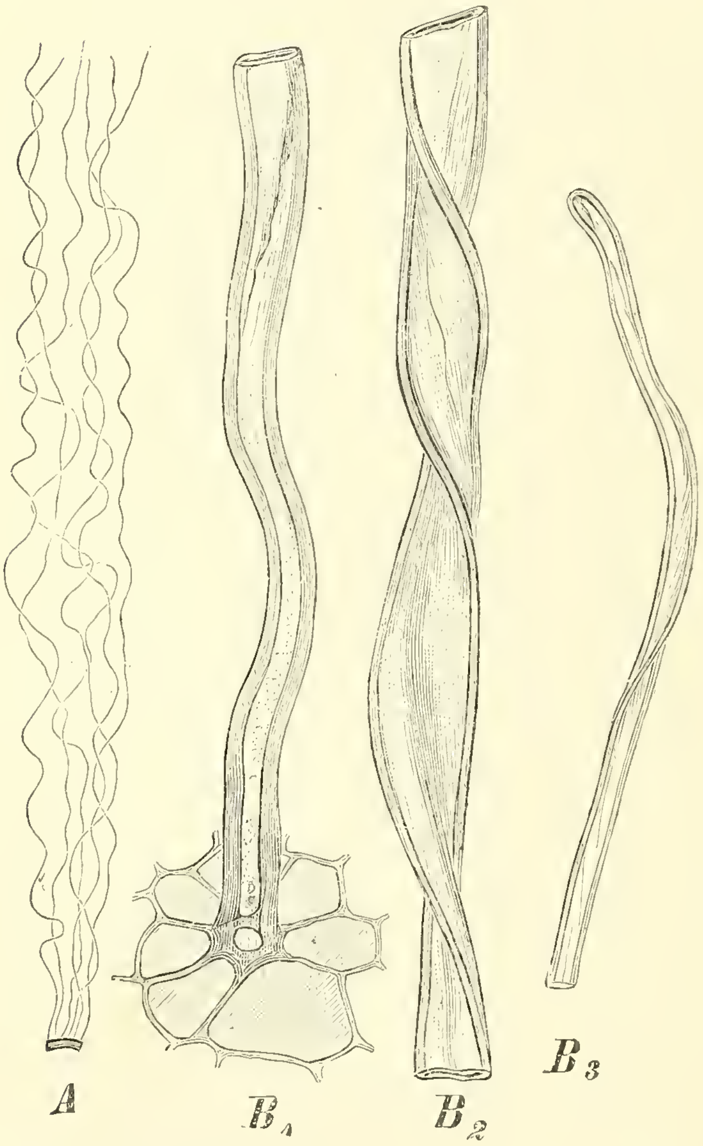


FIG. 114.—Seed-hairs of the cotton, *Gossypium herbaceum*. *A*, Part of seed-coat with hairs (× 3); B_1 insertion and lower part, B_2 middle part, and B_3 upper part, of a hair. (× 300.)

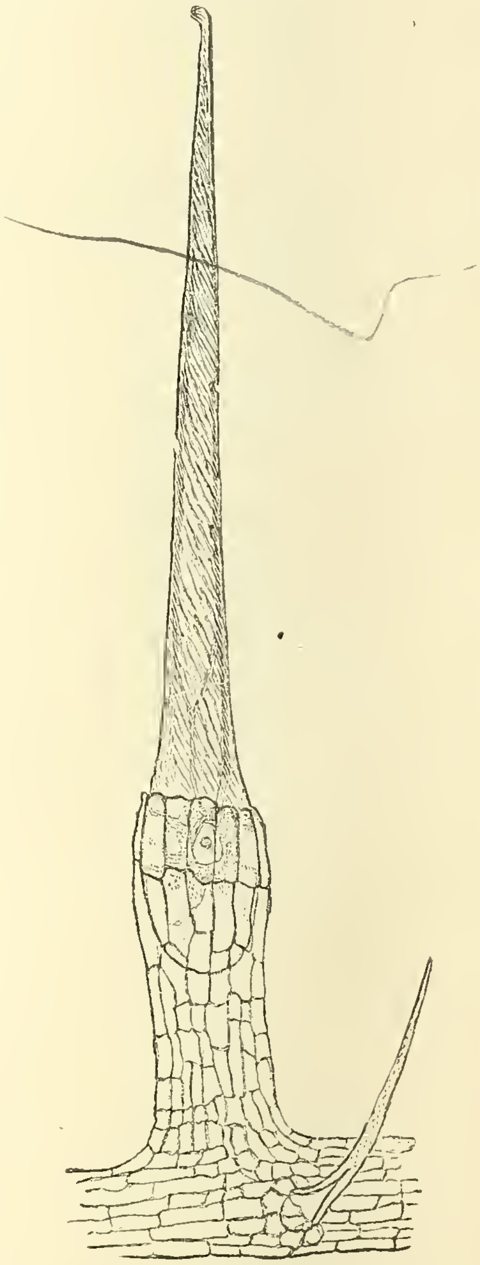


FIG. 115.—Stinging hair of *Urtica dioica*, with a portion of the epidermis, and, to the right, a small bristle. (× 60.)

appearance (Fig. 113). Longer hairs, such as the root-hairs (Fig. 53, *r*), are also prolongations of single epidermal cells; these retain their living contents. The soft, hairy growths found in young buds are generally similarly prolonged epidermal cells which, as a protective covering, surround the young growing tissues and sometimes remain on fully-developed plants to shield them from too rapid evaporation and sudden changes of temperature. The hairs developed from some of the epidermal cells of the seed coats of various species of *Gossypium* attain an unusual length, and supply the cotton of commerce (Fig. 114). These cotton hairs are sometimes 6 cm. long, and in their fully-developed state contain only air; their cell walls are thicker than those of ordinary hairs, and covered with a delicate cuticle. They are usually somewhat flattened and at the same time twisted; and are wider in the middle than at either end (Fig. 114, B_2). BRISTLES are short, pointed hairs, in the thickened cell walls of which calcium or silica has been deposited (Fig. 115, below, to the right).

The STINGING HAIRS (Fig. 115), such as those of Nettles (*Urtica*) and of the *Loasaceae*, are special forms of bristles, and arise as prolongations of single epidermal cells. These, however, swell in the course of their development, and becoming surrounded by adjoining epidermal cells present the appearance of being set in sockets; while, at the same time, by the multiplication of the cells in the tissue at their base, the whole hair becomes elevated on a column-like protuberance. The hair tapers towards the apex and terminates, somewhat obliquely, in a small head, just below which the wall of the hair remains unthickened. As the wall of the hair is silicified at the end and calcified for the rest of its length, the whole hair is therefore extremely stiff. Such hairs furnish a means of defence against animals. The heads break off at the slightest touch, and the hairs piercing the skin pour out their poisonous contents, which, especially in the case of the *Loasaceae*, may cause severe inflammation.

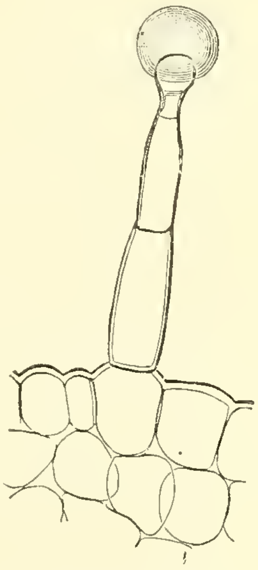


FIG. 116.—Glandular hair from the petiole of *Primula sinensis*. (After DE BARY, × 142.)

UNICELLULAR HAIRS, such as we have so far considered, may terminate in well-defined heads resulting from the swelling of their tips, or their side walls may develop irregular excrescences; on the other hand, they may remain short and expand like a balloon, or remain close to the surface of the epidermis as spindle-shaped or stellate hairs. MULTICELLULAR HAIRS may be merely simple rows of similar cells, as the hairs on the stamens of *Tradescantia* (Fig. 60); or their terminal cells may become swollen into globular heads (Fig. 116), like those on the Chinese Primrose (*Primula sinensis*); or an epidermis may be covered with shield-, star-, or bowl-shaped hairs (Fig. 117). Sometimes the hairs become variously branched, lose their living contents, and serve as a protective covering similar to that formed by unicellular hairs. In special cases, as in the scale hairs of Ferns, they may even have the shape of a small leaf.

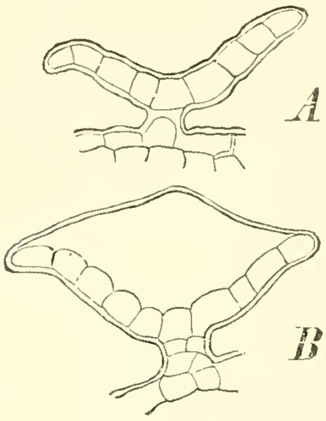


FIG. 117.—Glandular scale from the female inflorescence of the Hop. *Humulus Lupulus*, in vertical section. *A*, before, *B*, after the cuticle has become distended by the excretion. In *B* the excretion has been removed by alcohol. (After DE BARY, × 142.)

EMERGENCES, unlike hairs, are not formed solely by epidermal cells, but a number of cells, lying more or less deeply in the sub-epidermal tissues, also take part in their formation. Thus, for example, while only a few rows of sub-epidermal cells enter into the formation of the emergences (Fig. 118) on the margins of the stipules of the Pansy (*Viola tricolor*), much deeper-lying tissue participates in the development of the emergences which, as PRICKLES, serve in the case of roses as a means of protection, and at the same time are of assistance in climbing. The thick emergences, which spring from the roots of the *Podostemaceae*, and serve to attach them to rocks, are parenchymatous throughout, but vascular bundles may be included within the emergences, as is well shown in the club-shaped digestive glands or tentacles (Fig. 119) on the leaves of the Sundew (*Drosera*). Some emergences resemble in structure certain of the metamorphosed members of the plant body described in the preceding chapter; the resemblance between prickles and thorns, for instance, is particularly noticeable.

Both hairs and emergences sometimes act as secreting organs, and are then termed GLANDS. In many cases they are concerned with the active exudation, and at times also the absorption of water. They then belong to the class of organs designated HYDATHODES (^{58} a) by HABERLANDT. Other glandular hairs excrete a resinous substance. The hairs of *Primula sinensis* (Fig. 116) are in reality such glands, and it is from their excretions that the plant derives its peculiar odour. The cuticle of the terminal globular head is pressed away from the cell wall by the resinous

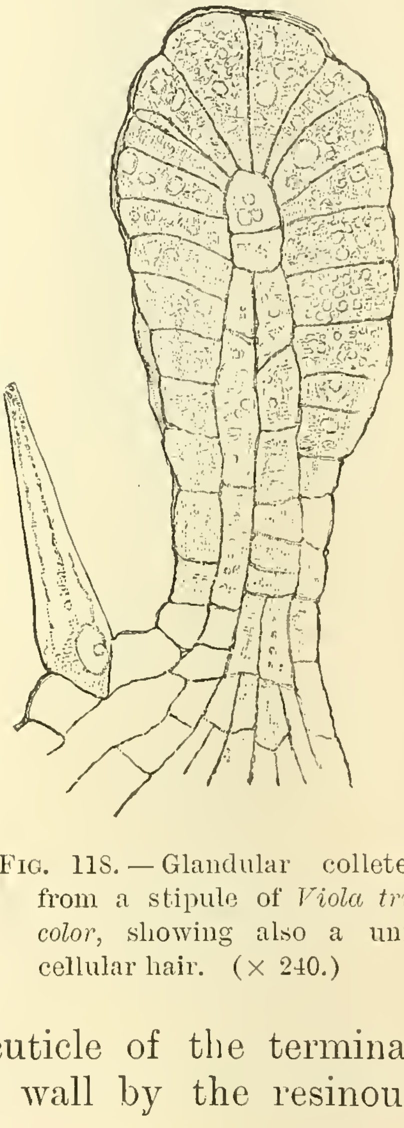


FIG. 118.—Glandular colleter from a stipule of *Viola tricolor*, showing also a unicellular hair. (× 240.)

matter excreted from the hair, until, finally, the bulging cuticle is ruptured and the resinous secretion exudes; the hairs of this and other species of *Primula* (especially *P. obconica*) are capable of exciting inflammation in the skin of those handling them (59). The similar but more complicated glandular hairs of Hops (Fig. 117) produce a secretion called LUPULIN, to which beer owes its bitter taste and distinctive aroma. The secretion is set free by the bursting of the cuticle, the latter having been previously pressed out from the underlying cell wall as a continuous membrane (Fig. 117, *B*). Hairs and emergences with abundant protoplasmic contents occur on irritable stamens, perianth leaves, and pulvini, and, as Haberlandt (58 b), showed, act as tactile papillæ, hairs, or bristles in the reception of stimuli. In other cases they are not themselves irritable, but serve to conduct a stimulus mechanically towards the irritable tissue.

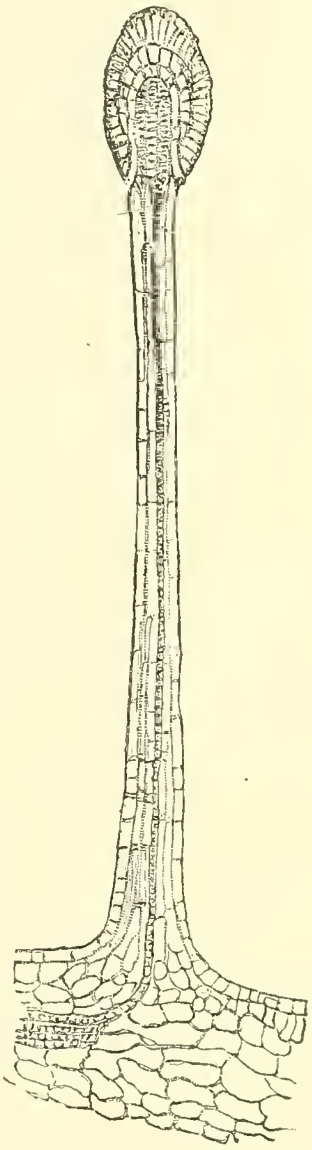


FIG. 119.—Digestive gland from *Drosera rotundifolia*. (× 60.)

The mucilaginous matter produced in young buds by the mucus papillæ or COLLETERS results from the partial dissolution of the cell wall under the cuticle. After the mucilaginous secretion has been discharged by the ultimate rupture of the cuticle, another new cuticle forms over the continually developing cell wall, and the process is again repeated. The colleters are but special forms of hairy structures, and are often developed in buds to protect the young organs from drying, by means of the mucilaginous modification of their cell walls. Where the dissolution of the cell wall is accompanied by secretions from the underlying cells, the colleters assume rather the character of glandular hairs. Such GLANDULAR COLLETERS are prevalent in the winter buds of trees; in the Horse-chestnut (*Aesculus Hippocastanum*), for example, the bud-scales of the winter buds are stuck together by a mixture of gum and resin, which has exuded from colleters of this nature. The glandular hairs of the Pansy (Fig. 118) act in a similar manner. The emergences on the leaves of the Sundew (*Drosera*), described as digestive glands (Fig. 119), discharge glistening drops of mucilaginous matter, not under the cuticle, but directly from the surface of the glands at the ends of the tentacles. Small animals are caught by means of these sticky excretions, and are afterwards digested by the plant. The nectaries also often excrete sugary solutions directly from their surfaces. In flowers these serve to attract insects, which effect pollination, while on other parts of the plant they are known in certain cases to attract ants, which protect the plant. The osmotically active substances in the nectar are in the first instance derived by transformation of the outer cell walls or are secreted by the cells. The presence of these substances on the surface of the nectary attracts water from the tissue beneath, and thus leads to the continued formation of the nectar.

In some of the *Piperaceae* and *Begoniaceae*, and in some species of *Ficus*, the epidermis is composed of several layers; but this is of comparatively rare occurrence. Such a many-layered epidermis results from a division of the young epidermal cells parallel to their external surface. The epidermis of *Ficus elastica* (Fig. 75) has three layers, and serves as a reservoir for accumulating water. The cystoliths of *Ficus elastica*, already referred to (p. 67), occur in considerably swollen epidermal cells. The multi-layered epidermis of the aerial roots of many Orchids, and of various Aroids, undergoes a peculiar modification and forms the so-called VELAMEN RADICUM (p. 45), a parchment-like sheath surrounding the roots, and often attaining a considerable thickness. The cells of this enveloping sheath are generally provided with spiral or reticulate thickenings, and lose their living contents. They then become filled with either water or air, depending upon the amount of moisture contained in the surrounding atmosphere. These root-envelopes absorb water like blotting-paper; when the velamen is filled with water, the underlying tissues impart a greenish tint to the root; but if it contains only air the root appears white. The epidermis of fruits, and particularly of seeds, exhibits a considerable variety of modifications in its mode of thickening, and in the relations the thickening layers bear to one another. The purpose of these modifications in the epidermis becomes at once evident, when it is taken into consideration that, in the case of flowers and seeds, in addition to protecting and enclosing their internal parts, the epidermis has often to provide for their dissemination and permanent lodgment.

The Vascular Bundle System.—The PRIMARY VASCULAR BUNDLES extend in the form of strands throughout the body of the higher plants. In more transparent stems, such as those of *Impatiens parviflora*, the bundles may be clearly distinguished and their direction followed. The arrangement of the bundles in leaves is apparent from their venation. In many parallel-veined leaves the bundles are easily isolated. This is often done accidentally, as when, for example, in picking a leaf of Plantain (*Plantago media*) a pull is given at the same time.

Special strands of tissue serving for the transport of substances through the plant are found in the more highly differentiated *Thallophyta*; examples are afforded by some of the Red and Brown Seaweeds (*Rhodophyceae* and *Phaeophyceae*). In the *Laminariaceae* these conducting tracts contain elements which closely resemble sieve-tubes (60). The thallus of many Liverworts is traversed by a strand which resembles the nerve of a leaf. Bundles sharply limited from the surrounding tissues first appear in the Mosses; they occur commonly in the leaves, less often in the stems. A fairly simple example of this kind of conducting bundle is that of the stem of *Mnium undulatum*, which is represented in transverse section in Fig. 160. Such bundles reach their highest differentiation in the *Polytrichaceae*. In them the stem contains a central cylinder composed of elongated empty tubes, of elements resembling sieve-tubes, and of elongated cells; the three kinds of element serve respectively to transport water, albuminous substances, and carbohydrates (61). The arrangement of the tissue of these complicated strands is often similar to that found in the vascular bundles of more highly organised plants. This is a good example of a striking resemblance between structures which are analogous but have arisen independently in the course of evolution.

It is, however, in the Cormophytes, which possess roots, that a high degree of differentiation of the vascular bundles is attained. Since the absorption of water is limited to the roots, the arrangements in the conducting tracts require to be more perfect. Two distinct portions can be distinguished in these vascular bundles, the TRACHEAL or XYLEM PORTION, and the SIEVE or PHLOEM PORTION. While each portion may form independent strands, they are generally united in one VASCULAR BUNDLE (Figs. 120-122). Other terms often used to designate the vascular bundles are FIBRO-VASCULAR BUNDLES and MESTOME. The vascular portion is also termed the XYLEM or HADROME, and the sieve-tube portion the PHLOEM or LEPTOME (^{62}). The vascular portion contains TRACHEÆ and TRACHEIDS as most essential for the fulfilment of its function as a water conductor (*a*, *sp*, *m*, Figs.

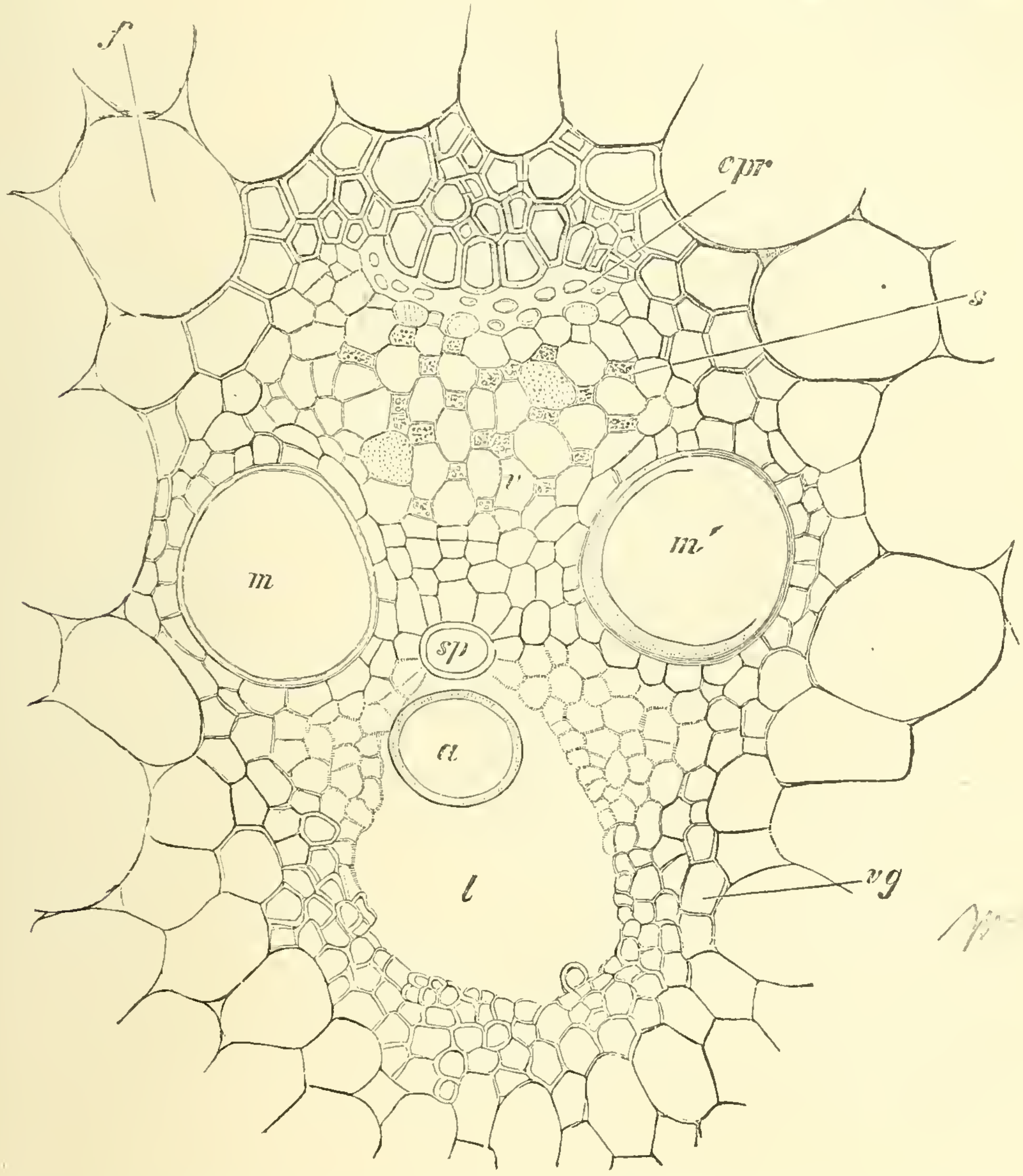


FIG. 120.—Transverse section of a vascular bundle from the internode of a stem of *Zea Mais*. *a*, Ring of an annular tracheid; *sp*, spiral tracheid; *m* and *m′*, vessels with bordered pits; *v*, sieve-tubes; *s*, companion cells; *cpr*, compressed protophloem; *l*, intercellular passage; *vg*, sheath; *f*, cell of fundamental tissue. (× 180.)

120, 121), or tracheids alone, and, in addition, living, elongated parenchymatous cells that may be designated XYLEM or WOOD PARENCHYMA. In the phloem portion the most essential elements are the SIEVE-TUBES (*v*), which serve for the conveyance of albuminous matter. They are always accompanied by other living cells; either by the so-called COMPANION CELLS (*s*), or in addition by elongated parenchymatous cells, or by the parenchyma alone. The companion cells are sister cells of the sieve-tubes, for both have arisen by longitudinal division from the same mother cell. The companion cells are not so large as the sieve-tubes, and may be distinguished from them by their more abundant protoplasmic contents, and especially by the fact that they retain their nuclei, while the nuclei of the sieve-tubes soon disappear. In Monocotyledons (Figs. 120, 121), and in the *Ranunculaceae* among the Dicotyledons (Fig. 122), the phloem consists solely of sieve-tubes and companion cells; in the other Dicotyledons parenchymatous elements are also present, and these are accordingly distinguished as PHLOEM OR SIEVE PARENCHYMA; no companion cells are found in Gymnosperms and Pteridophytes, and in addition to sieve-tubes the phloem contains only phloem parenchyma.

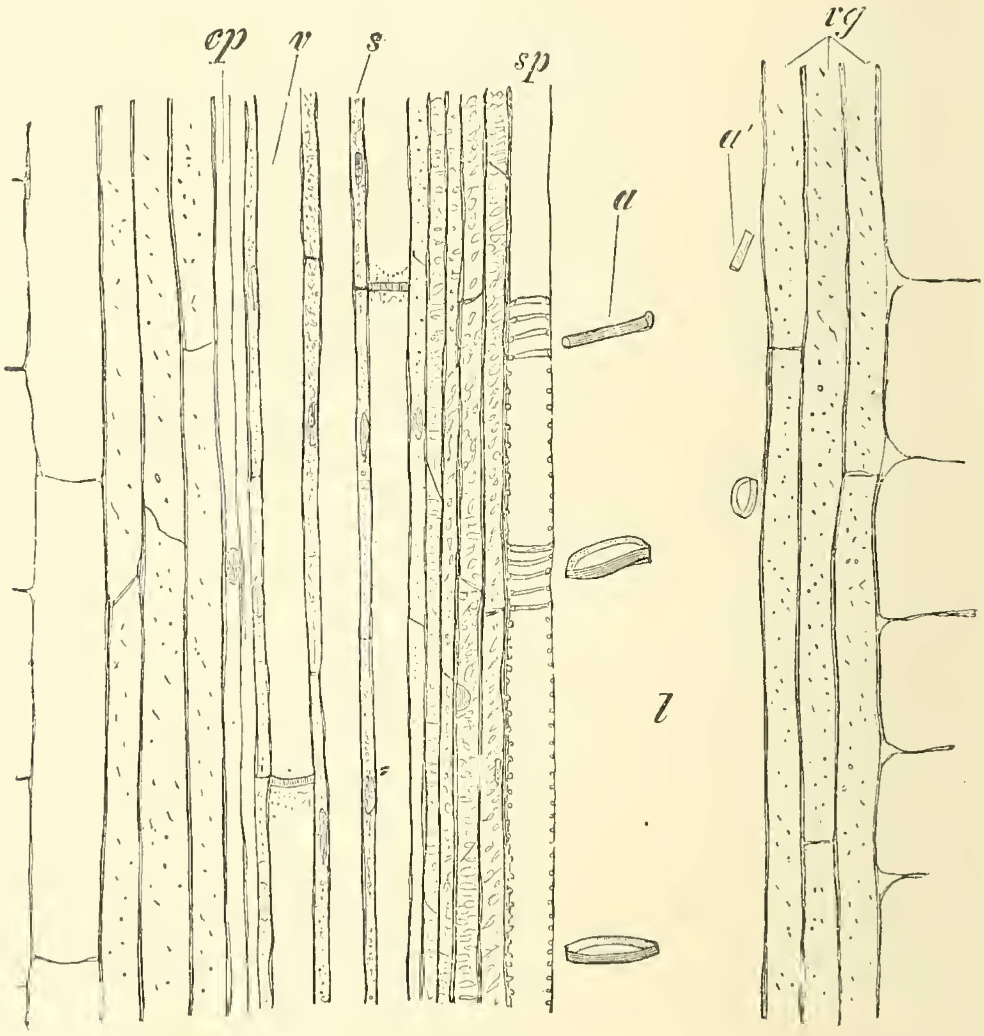


FIG. 121.—Longitudinal section of a vascular bundle from the stem of *Zea Mais*. *a*, and *a'*, Rings of an annular tracheid; *v*, sieve-tubes; *s*, companion cells; *cp*, protophloem; *l*, intercellular passage; *vg*, sheath; *sp*, spiral tracheids. (× 180.)

The bundles of the Phanerogams (Gymnosperms and Angiosperms) are generally COLLATERAL in structure, that is, the xylem and phloem are in contact on one side only. In stems the most usual arrangement of the two portions of a collateral bundle is that in which the xylem lies nearest the centre; in leaves the xylem portion lies nearer the upper, and the phloem portion nearer the lower surface. Closely allied to the collateral type is the bicollateral type of bundle. In the latter the xylem is accompanied by phloem on each side, both on the outside and inside. Such bicollateral bundles are characteristic of the *Cucurbitaceae*, but occur also in several other families of Dicotyledons. The xylem and phloem of roots generally form separate strands (Fig. 123, *s*, *v*), and in that case the arrangement of the vascular portion is somewhat altered; for, while in stems the narrow vessels of the xylem are nearer the centre and the wider nearer the circumference, in roots this order is exactly reversed.

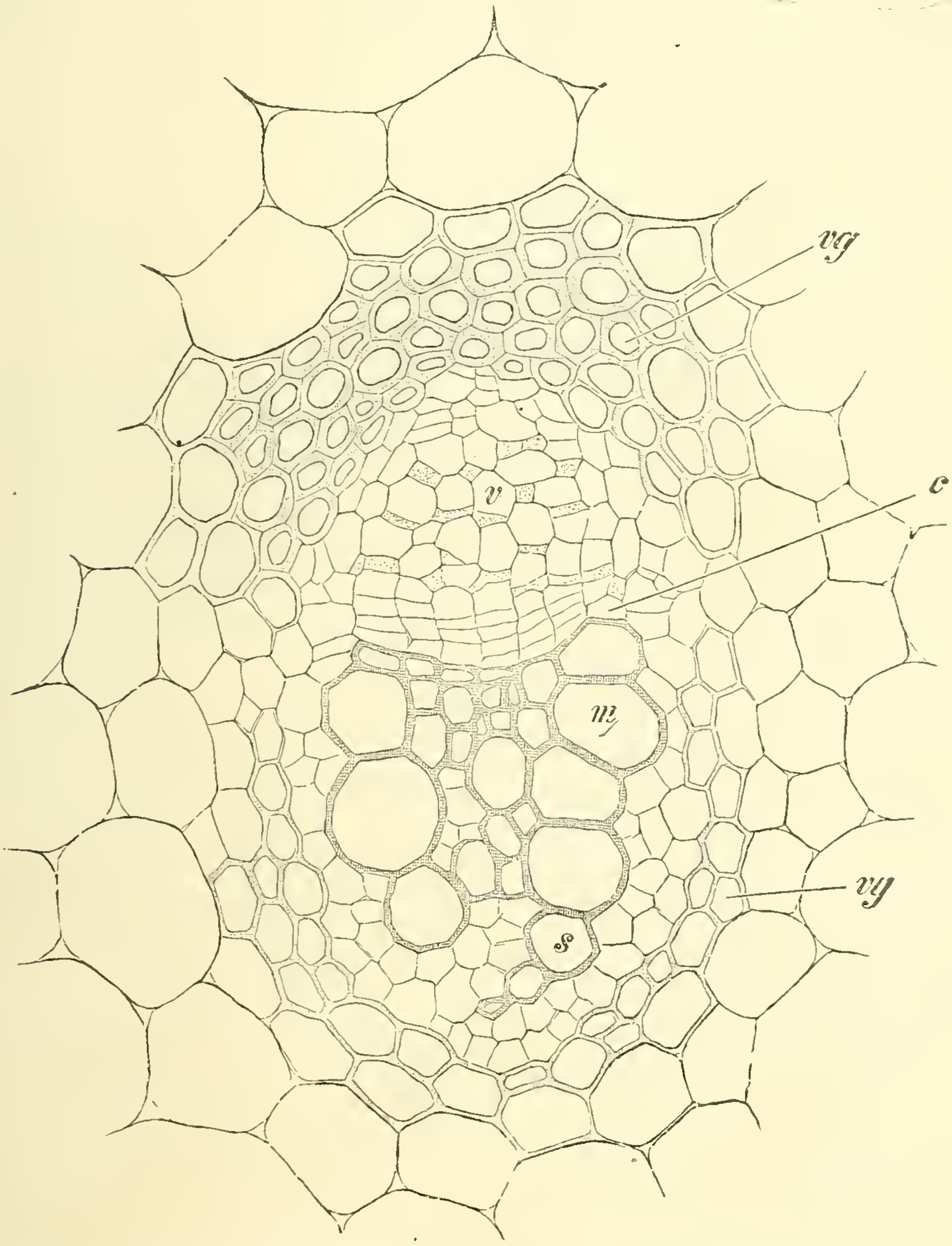


FIG. 122.—Transverse section of a vascular bundle from a stolon of *Ranunculus repens*. *s*, Spiral tracheids; *m*, vessel with bordered pits; *c*, cambium; *v*, sieve-tubes; *vg*, sheath. (× 180.)

The vascular bundle strands of the Pteridophytes (Fig. 124), although usually termed CONCENTRIC bundles, cannot be compared with the single vascular bundles of the Phanerogams, but correspond rather to an aggregated complex of such bundles. The centre of such a vascular bundle strand consists of tracheids (*sp*), and also, in special instances, of tracheæ (*sc*). These elements show typical scalariform markings, and only the very smallest are spirally thickened (*sp*). The xylem parenchyma (*lp*) surrounds the tracheal elements, while both are encircled by phloem consisting of sieve-tubes (*v*) and phloem parenchyma (*s*).

Such vascular bundle strands occur in the Ferns and *Selaginellaceae*, and also in the *Lycopodiaceae*, where they exhibit even a greater degree of coalescence. In the *Equisetaceae* the vascular bundles correspond more nearly to the collateral bundles of the Phanerogams.

The vascular bundles are developed from strands of meristematic tissue which are called PROCAMBIUM STRANDS. If the whole meristematic tissue of a procambium strand is exhausted in this process, the finally-developed vascular bundles are said to be CLOSED; but if any of the meristematic tissue remains in an undifferentiated condition between the xylem and phloem portions, the bundles are spoken of as OPEN. The Pteridophytes have, almost without exception, closed bundles; in Monocotyledons also the bundles are always closed (Fig. 120); Gymnosperms and Dicotyledons, on the contrary, have open bundles (Fig. 122). The meristematic tissue which remains undifferentiated between the xylem and phloem portions of a bundle is called the CAMBIUM (Fig. 122).

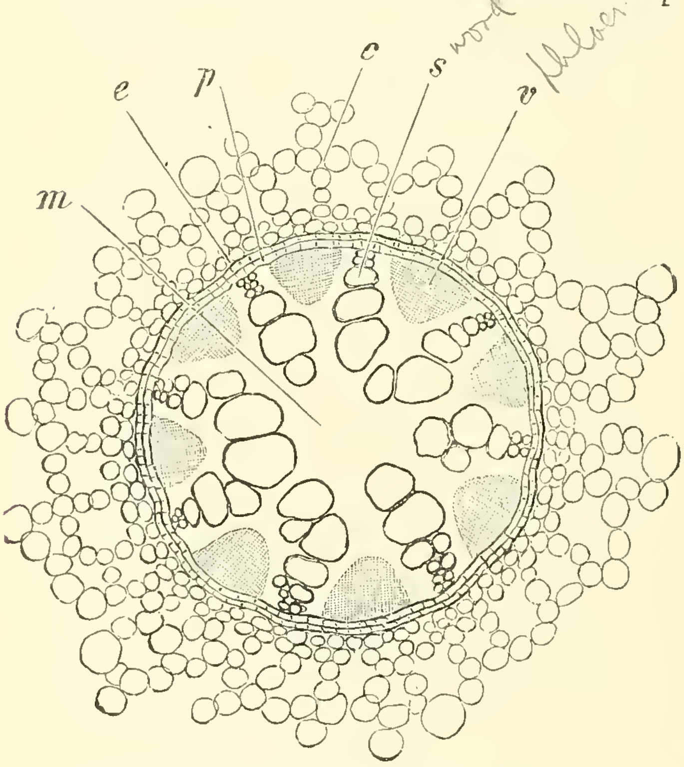


FIG. 123.—Transverse section of central portion of the root of *Acorus Calamus*. *m*, Medulla; *s*, xylem; *v*, phloem; *p*, pericycle; *e*, endodermis; *c*, cortex. (× 90.)

In those portions of plants which still retain an energetic vertical growth, the procambium strands remain undifferentiated, except at definite points, where single rows of cells lose their meristematic condition and form narrow, annular, and spiral vessels and sieve-tubes, or sieve-tubes and companion cells, the structure of all of which is of such a nature as to render their elongation possible. Such primary vascular elements are termed PROTOXYLEM; while the corresponding sieve elements are in like manner designated PROTOPHLOEM. The protoxylem occupies the innermost, the protophloem the outermost side of a procambium strand, from which a collateral bundle is eventually formed. After the vertical growth of any part of a plant ceases, the differentiation of the procambium strand into a collateral vascular bundle is continued from the inner and outer sides of the strand toward the centre.

In fully-developed vascular bundles the protoxylem and protophloem cease to perform their functions. The protoxylem elements become compressed and ruptured by the tension resulting from the continued vertical growth (*a* and *a'*, Fig. 121), so that in their stead a lysigenic intercellular space is often formed (Figs. 120, 121).

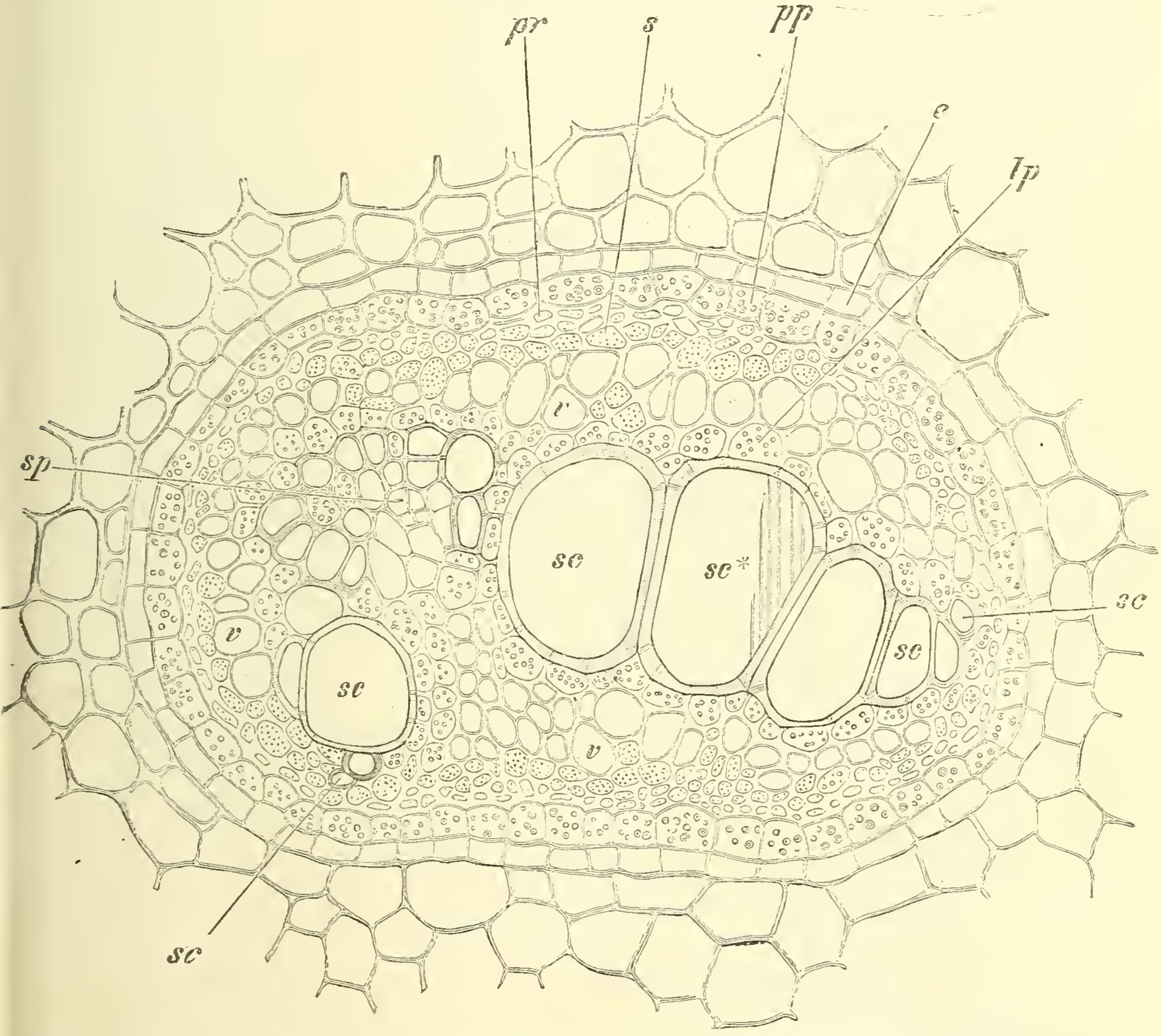


FIG. 124.—Transverse section of the vascular-bundle cylinder of the petiole of *Pteris aquilina*. *sc*, Scalariform vessels; *sp*, protoxylem; *sc**, part of a transverse wall showing scalariform perforations; *lp*, xylem parenchyma; *v*, sieve-tubes; *pr*, protophloem; *pp*, starch layer; *e*, endodermis; *s*, phloem parenchyma. (× 240.)

The protophloem elements (cf. Figs. 120, 121) at the same time become disorganised, and their sieve-plates closed by a covering of callus.

In accordance with the orientation of the xylem, the protoxylem of roots is found on the outer, not on the inner side of the vascular strands (Fig. 123).

The Terminations of the Vascular Bundles.—In leaves, particularly in the deciduous leaves of Angiosperms, the vascular bundles become much branched until finally they are reduced to extremely fine strands. In the leaves of Gymnosperms this branching of the bundles does not usually take place, but instead, a single vascular bundle frequently runs throughout the whole length of the leaf. The vascular bundles of the reticulate-veined leaves of Dicotyledons illustrate the most extreme form of branching.

The fine distribution of the bundles in the leaf-lamina facilitates the regular conduction of water to all parts of the leaf-tissue, and at the same time renders easier the removal of the assimilated products. An extended distribution of the bundles in the leaves is thus evidently of advantage to a plant. In the same degree as the ramifications of the vascular bundles are continued, the bundles themselves become attenuated and simpler in structure (Fig. 125). The vessels first disappear, and only spirally and reticulately thickened tracheids remain to provide for the water conduction. The phloem elements undergo a similar reduction. In Angiosperms, in which the sieve-tubes are accompanied by companion cells, the sieve-tubes become narrower, whilst the companion cells retain their original dimensions. Finally, in the cells forming the continuation of the sieve-tubes, the longitudinal division into sieve-tubes and companion cells discontinues, and TRANSITION CELLS are formed (63). With these the sieve-tubes terminate, although the vascular portion of the bundles still continues to be represented by short spiral tracheids, until finally they too disappear, either terminating blindly or anastomosing with other vascular bundles.

The Fundamental Tissue System usually forms the principal part of the primary tissues of the body of a plant. The whole tissue of the lower plants, as it shows no internal differentiation, may, in a certain sense, be considered fundamental tissue. The other tissues have gradually been developed from the fundamental tissue in the course of phylogenetic development. The fundamental tissue in the higher plants is enclosed by tegumentary tissue, and traversed by the vascular bundle system. While the tegumentary tissue protects the plant externally, and the vascular bundle system performs the office of conduction, and also of mechanically strengthening the plant, the duty of providing for the nutrition of the plant and of storing reserve food material falls chiefly to the fundamental tissue. The fundamental tissue consists, therefore, for the most part of parenchymatous cells containing chlorophyll, at least to such depth as the light penetrates; but internally, and wherever the tissues are so situated as to be unaffected by the influence of the light, a colourless parenchyma is found. The fundamental tissue system also takes part in providing

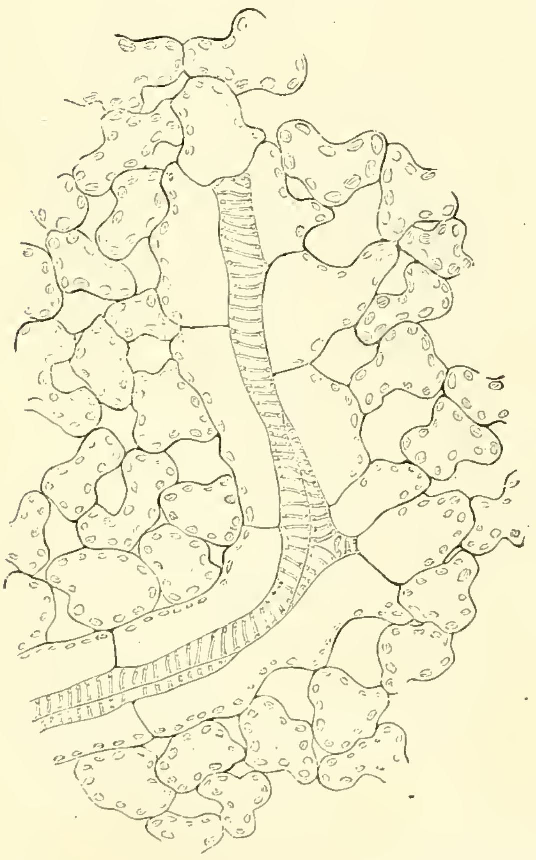


FIG. 125.—Termination of a vascular bundle in a leaf of *Impatiens parviflora*. (× 240.)

for the mechanical rigidity of plants, and in connection with this function it possesses collenchyma (Fig. 74, *c*) and sclerenchyma as its special mechanical tissues. The COLLENCHYMA is unlignified and very elastic, and thus fitted for stretching; it is the form of mechanical tissue suitable for those parts of plants still undergoing growth in length. The sclerenchymatous fibres, on the other hand, are formed after growth in length has ceased, and sclereids (p. 71) arise even later. The elongated cells of the fundamental tissue also perform a certain share of the work of conduction, and are specially active in the transport of carbohydrates. Secondary or waste products, resulting from chemical changes, are also deposited in special cells of the fundamental tissue. Consequently idioblasts (p. 71), containing crystals or rows of crystal-containing cells, are often met with in the fundamental tissues, together with cells, tubes, cavities, or canals containing tannin, gum, resin, ethereal oils, latex, or alkaloids. Such waste products are for the most part deposited near the surface of a plant, in order to serve as a defence against destructive animals, or that they may afterwards be thrown off along with the superficial tissue. Cells containing these waste products, particularly crystal cells and latex tubes, are often found, therefore, accompanying the phloem portion of the vascular bundles.

The *Aroideae*, *Nymphaeaceae*, and several other plant families possess a peculiar form of idioblasts, the so-called internal hairs, which project into the intercellular spaces of the fundamental tissue. In the wide intercellular passages of the leaf and flower stems of the Water-Lily these idioblasts are stellate in form. Their walls are strongly thickened, and provided with short protuberances in which small crystals of calcium oxalate are deposited.

The Distribution of the Primary Tissues (64)

In the body of multicellular plants a distinction between an outer small-celled and firm tissue and an inner large-celled looser tissue soon becomes apparent. The outer tissues are best adapted for protection, the inner for conduction and storage. The cells of the inner tissues accordingly become elongated for the purpose of conduction. The outer tissues in plants, which must provide independently for their own nourishment, contain chromatophores fitted for assimilation, and are correspondingly coloured, while the inner tissues remain colourless. The outer portion of the fundamental tissue thus differentiated is called the CORTEX, the inner the MEDULLA or PITH. An epidermis, distinguishable from the cortex, is found in some of the Mosses, but a sharp distinction between these tissues is first found in the more highly organised plants.

In the **Stem** of a Phanerogamic plant there is an outer skin or epidermis (Fig. 127, *e*) on the external surface; then follows the PRIMARY CORTEX (Figs. 126, 127, *pr*), and internal to this the so-called

CENTRAL CYLINDER, for which VAN TIEGHEM has proposed the name STELE (column). The innermost layer of the primary cortex, which may be designated by the term PHLOEOTERMA, is for the most part not distinctly differentiated, but can be recognised in the aerial stems of land-plants as a starch-sheath; while in the rhizomes of land-plants and in the stems of water-plants it forms the ENDODERMIS. Differentiated as a starch-sheath (Fig. 127, *st*), the phloeoterma is rendered conspicuous by the quantity of starch contained in its cells; when developed as an endodermis, portions of the lateral walls of its cells become suberised. In a cross-section these suberised portions of the cell walls of the endodermis appear as dark spots (Fig. 128), but in a tangential section as sinuous lines. The STELE or CENTRAL CYLINDER of the stem contains vascular bundles (*cv*), which, in the *Equisetaceae* and some other Pteridophytes, as well as in the Gymnosperms and Dicotyledons (Fig. 127), are arranged in a circle, whereas in Monocotyledons (Fig. 126) they are irregularly distributed. In all these cases the xylem portion of the vascular bundle is directed towards the centre, and the phloem portion away from the centre of the stem. That part of the peripheral tissue of the central cylinder lying to the outside of the bundles is called the PERICYCLE (*pc*). If the bundles are arranged in a circle (Fig. 127), that part of the central cylinder enclosed by them is the PITH or MEDULLA (*m*), and the tissue between the different bundles the PRIMARY MEDULLARY RAYS (*ms*). In the case of scattered bundles (Fig. 126), a distinction between medulla and

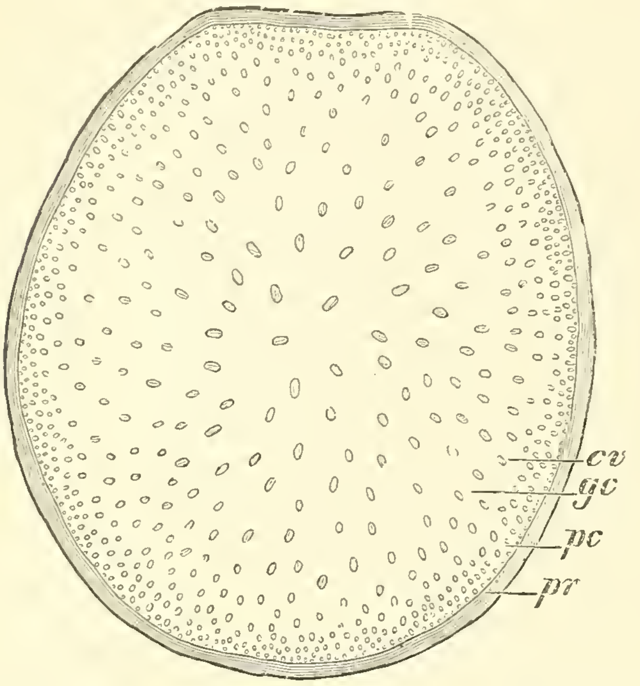


FIG. 126.—Transverse section of an internode of the stem of *Zea Mais*. *pr*, Primary cortex; *pc*, pericycle; *cv*, vascular bundles; *gc*, fundamental tissue of the central cylinder. (× 2.)

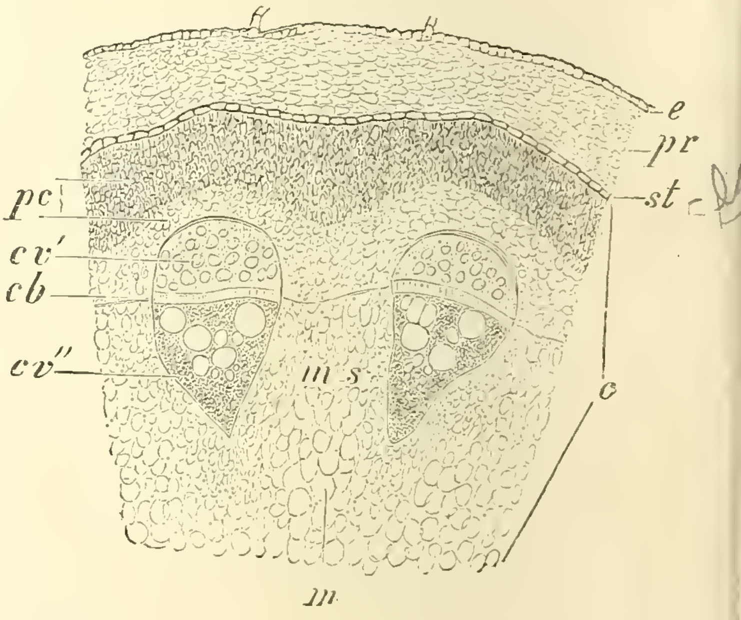


FIG. 127.—Part of a transverse section of a young stem of *Aristolochia Sipho*. *e*, Epidermis; *pr*, primary cortex; *st*, starch-sheath; *c*, central cylinder; *pc*, pericycle, in this case with a ring of sclerenchyma fibres; *cv′*, phloem, and *cv″*, xylem portions of the vascular bundle; *cb*, cambium ring; *m*, medulla; *ms*, primary medullary ray. (× 48.)

medullary rays is no longer possible, and the whole tissue surrounding the bundles must then be considered as corresponding to the primary medullary rays. The division of the tissue systems in the stems of the higher plants into epidermis, primary cortex, and central cylinder, brings with it a corresponding division of the fundamental tissue into the fundamental tissue of the primary cortex and the fundamental tissue of the central cylinder. Wherever there is no sharp distinction between primary cortex and central cylinder, comparative investigation alone can determine whether a tissue belongs to the primary cortex or to the central cylinder.

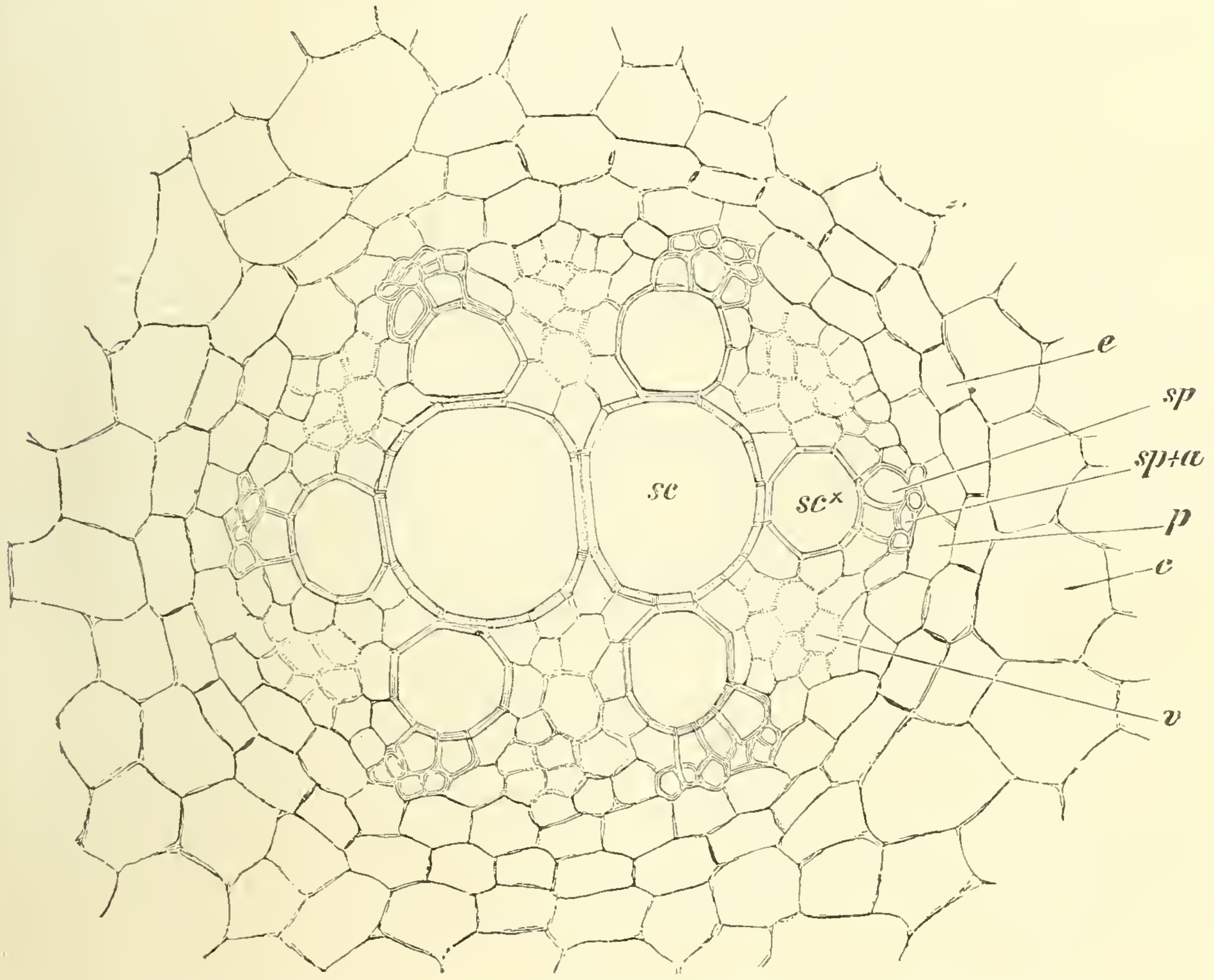


FIG. 128.—Transverse section of an adventitious root of *Allium Cepa*. *c*, Primary cortex ; *e*, endodermis ; *p*, pericycle ; *a*, annular tracheids ; *sp*, spiral tracheids ; *sc* and sc^*, scalariform vessels ; *v*, phloem. (× 240.)

Although the fundamental tissue of the primary cortex is pre-eminently a chlorophyll-containing tissue, portions bordering on the epidermis frequently become converted, for mechanical purposes, into strands of collenchyma or sclerenchyma. Such a mechanical tissue, which serves to strengthen the epidermis, is known as a HYPODERMA. Of the tissues composing the central cylinder, the pericycle, the primary medullary rays, and medulla consist of fundamental tissue, and are chiefly composed of colourless parenchyma. A part, however, of the tissue of the pericycle may become sclerenchymatous (Fig. 127, *pc*) ; sclerenchymatous elements also often surround individual bundles as sheaths, or accompany the phloem portion in the form of strands (Figs. 120, 122). Whenever such a sheath of sclerenchyma is developed about a bundle, it is always interrupted on both sides of the bundle, at the junction of the xylem and phloem portions, by parenchymatous cells, or by cells which are only slightly thickened and lignified. These cells facilitate the exchange of water and food material between the vascular bundles and the fundamental tissue, and are spoken of as TRANSFUSION STRANDS.

In the case of Phanerogams the central cylinder is simple and occupies a more or less central position. In some few instances, however, it breaks up into several partial cylinders or SCHIZOSTELES. Such schizosteles are found in the stems of *Auricula* and *Gunnera*. The tissue that surrounds and separates these central cylinders corresponds to the primary cortex.

The vascular bundle strands (p. 108) of the Pteridophytes are also to be regarded as schizosteles. In the stems of Ferns they are usually separated from one another (Fig. 129) and situated in the fundamental tissue belonging to the primary cortex. This is also the case in the Selaginellas. In *Lycopodium* (Fig. 130), on the contrary, the schizosteles become united into a single central cylinder.

Among the Ferns, also, *Osmunda regalis* has a single central cylinder, but this must not be regarded as derived from the fusion of several steles such as most ferns possess. It rather corresponds to a single cylinder occupying a central position in which a parenchymatous pith has originated within the vascular tissue. Parenchymatous rays also extend from this pith and divide the vascular tissue into a number of portions arranged in a single ring; the structure of this stele thus indicates the way in which a ring of collateral bundles can arise from a solid stele. According to Zenetti (65) a continuous zone of phloem is present in *Osmunda* to the outside of the separate groups of xylem; in the *Equisetaceae* (Fig. 348), on the other hand, the medullary rays extend through the phloem. Thus the latter plants possess a typical ring of separate collateral vascular bundles, such as is found in Gymnosperms and Dicotyledons.

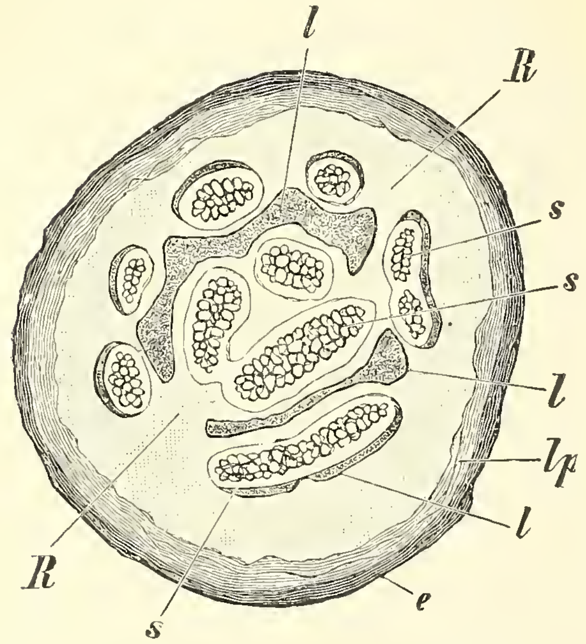


FIG. 129.—Transverse section of the rhizome of *Pteris aquilina*. *s*, Vascular bundle strands (schizosteles); *l*, sclerenchymatous plates; *lp*, peripheral zone of sclerenchymatous fibres; *R*, cortex; *e*, epidermis. (× 7.)

In **Roots**, the division between primary cortex and central cylinder is sharply marked by the endodermis, into which the innermost layer of the primary cortex is usually transformed (Figs. 123, 128, *e*). The central cylinder becomes completely shut off from the primary cortex by the suberisation of the lateral walls of the endodermal cells, and by their close and uninterrupted contact. While, by this means, the passage of gases from the intercellular spaces of the cortex into the central cylinder, and the consequent obstruction of the water-channels, are prevented, the passage of water from the cortex to the central cylinder can, at the same time, go on unhindered through the unsuberised inner and outer walls of the endodermal cells. In this manner it is possible for the water, absorbed from the soil by the root-hairs or by the surface of the roots, to be transferred to the tissues of the central cylinder. In the older parts of the roots, which no longer absorb water from the soil, the cells of the endodermis become greatly thickened, but generally on one side only. Should the thickening occur at an early stage, then special endodermal cells, directly external to the xylem strands, remain unthickened and serve as TRANSFUSION CELLS (Fig. 131, *f*).

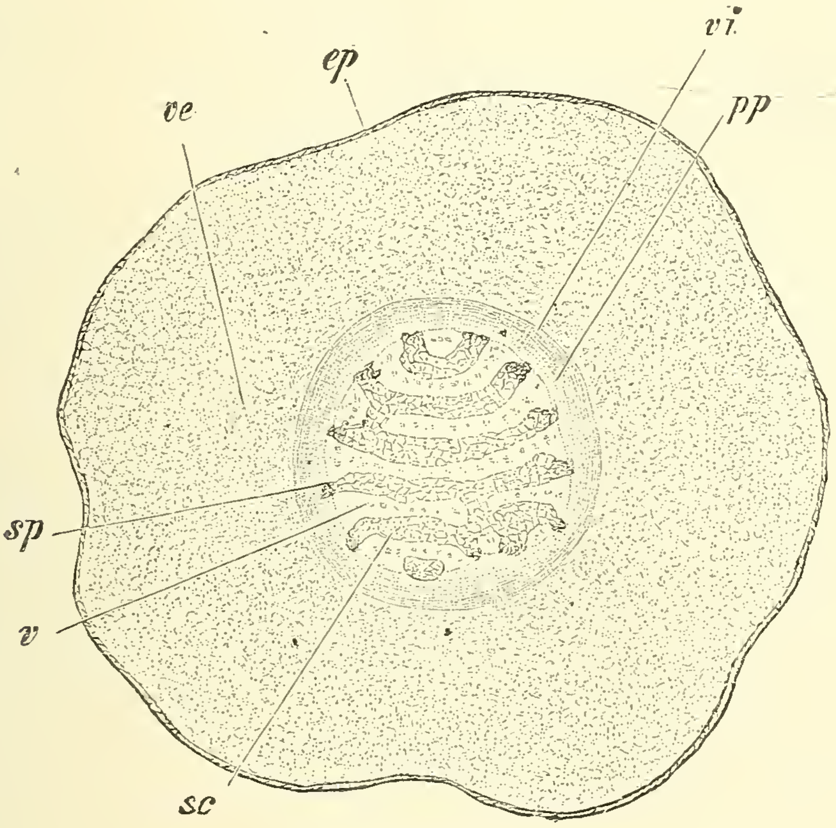


FIG. 130.—Transverse section of stem of *Lycopodium complanatum*. *ep*, Epidermis; *ve*, *vi*, *pp*, outer, inner, and innermost parts of the primary cortex, surrounding the central cylinder; *sc*, scalariform tracheids; *sp*, annular and spiral tracheids; *v*, phloem. (× 26.)

While the root-hairs are as a rule developed from the cells of the epidermis, they may, in case the epidermis is thrown off with the root-cap, arise from the outermost cortical layer, which then assumes the functions of an epidermis. In any case the epidermis ultimately disappears, and the outermost cortical layer becomes cuticularised and, as an EXODERMIS, takes its place. In aerial roots the epidermis may become converted into a many-layered tracheidal ROOT-SHEATH (p. 104).

The PRIMARY CORTEX OF ROOTS is composed of colourless tissue, which, with few exceptions, consists wholly of parenchyma. Although the cells of the outer layers of the cortex are uninterruptedly in contact with one another, the inner layers are often provided with intercellular air cavities or passages. The outer layer of cells (Figs. 123, 128, 131, *p*) of the CENTRAL CYLINDER OF ROOTS often forms the pericycle (pericambium) (66); this usually consists of a single layer of cells, but may be many-layered or entirely absent. The xylem and phloem portions form separate strands (p. 107), radially disposed and alternating with each other (Figs. 123, 128).

It has already been shown that the narrowest elements of the vascular strand are outermost. Roots are described as diarch, triarch, polyarch, according to the number of the radiating vascular strands. For example, the roots of *Acorus Calamus* (Fig. 123) are octarch, those of *Allium Cepa* (Fig. 128) hexarch. The vascular strands may either meet in the centre (Fig. 128), or they may surround a central pith (Fig. 123). Like the corresponding tissue in the stem, the fundamental tissue between the xylem and phloem strands may be termed primary medullary ray tissue.

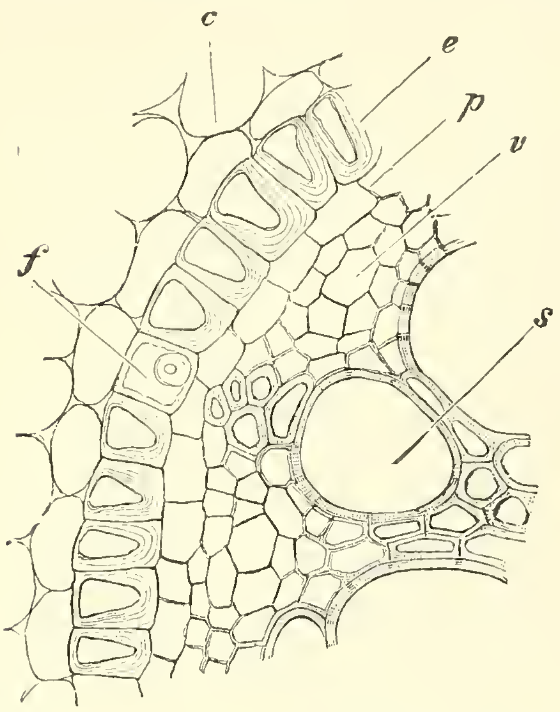


Fig. 131.—Part of a transverse section of a root of *Iris florentina*. *e*, Endodermis, showing cell walls thickened on one side; *f*, transfusion cell; *p*, pericycle; *v*, phloem; *s*, vessel of xylem: *c*, cortex. (× 240.)

The **Leaves** are composed of fundamental tissue (which is here termed mesophyll), bounded by an epidermis and traversed by vascular bundles. Sheaths are present around the bundles, extending to their fine terminations. The cells composing these mesophyll sheaths are as a rule elongated and not separated by intercellular spaces. Besides limiting the vascular bundles from the mesophyll, the sheaths perform the important function of conducting soluble carbohydrates from the leaf to the stem. The larger vascular bundles are usually accompanied by strands of sclerenchyma; these disappear from the finer branches. Other strands of sclerenchyma not connected with the vascular bundles may also occur in the mesophyll and contribute to the rigidity of the leaf.

The mesophyll passes into the primary cortex of the stem, while the vascular bundles are continuous with the central cylinder. Thus in the leaf, tissues corresponding to the cortex and central cylinder of the stem remain distinct from one another.

The mesophyll of the coloured FLORAL LEAVES of the Angiosperms usually consists of a somewhat loose tissue, containing intercellular spaces and traversed by vascular bundles. The laminæ of many assimilating FOLIAGE LEAVES, especially of shade-loving plants, may have a similar uniform structure; but they are usually more complicated, and exhibit a difference in the structure of their upper and lower sides (Fig. 132). They are, accordingly, dorsiventral, and, in correlation with this difference in structure, their two surfaces react differently toward external influences. In such dorsiventral structures the upper epidermis is succeeded by one or more layers of cylindrical parenchymatous elements elongated at right angles to the surface, and known as the PALISADE CELLS. These are especially rich in chlorophyll, and have only small intercellular spaces. Adjoining the palisade parenchyma, and extending to the epidermis (*ep''*) on the under surface of the leaf, is a loose tissue called the SPONGY PARENCHYMA. In contrast to the palisade cells, the cells of the spongy parenchyma are less abundantly supplied with chlorophyll; they are also much more irregular in shape, and enclose large intercellular air-spaces. The palisade cells are elongated in the direction in which the rays of light penetrate the leaf-lamina, and by this means are particularly adapted to their special function of assimilation. The spongy parenchyma, on the other hand, is arranged to facilitate the free passage of gases, and to that end develops large intercellular spaces in direct communication with the stomata of the under epidermis. HABERLANDT (67) has estimated that to every square millimetre of surface in a leaf of *Ricinus communis* there are, in the palisade cells, 403,200 chlorophyll granules; in the cells of the spongy parenchyma only 92,000; that is, 82 per cent of all the chlorophyll granules belong to the upper surface of the leaf, and only 18 per cent to the under side. The palisade cells are often arranged in groups, in which the lower ends of the cells of each group converge (Fig. 132). In this way several palisade cells come into direct contact with a single expanded cell of the spongy parenchyma, which thus functions, apparently, as a collecting cell for a group of palisade cells. The products of assimilation are passed on from the collecting cell through the spongy parenchyma, to be finally carried to the mesophyll sheath surrounding the vascular bundles.

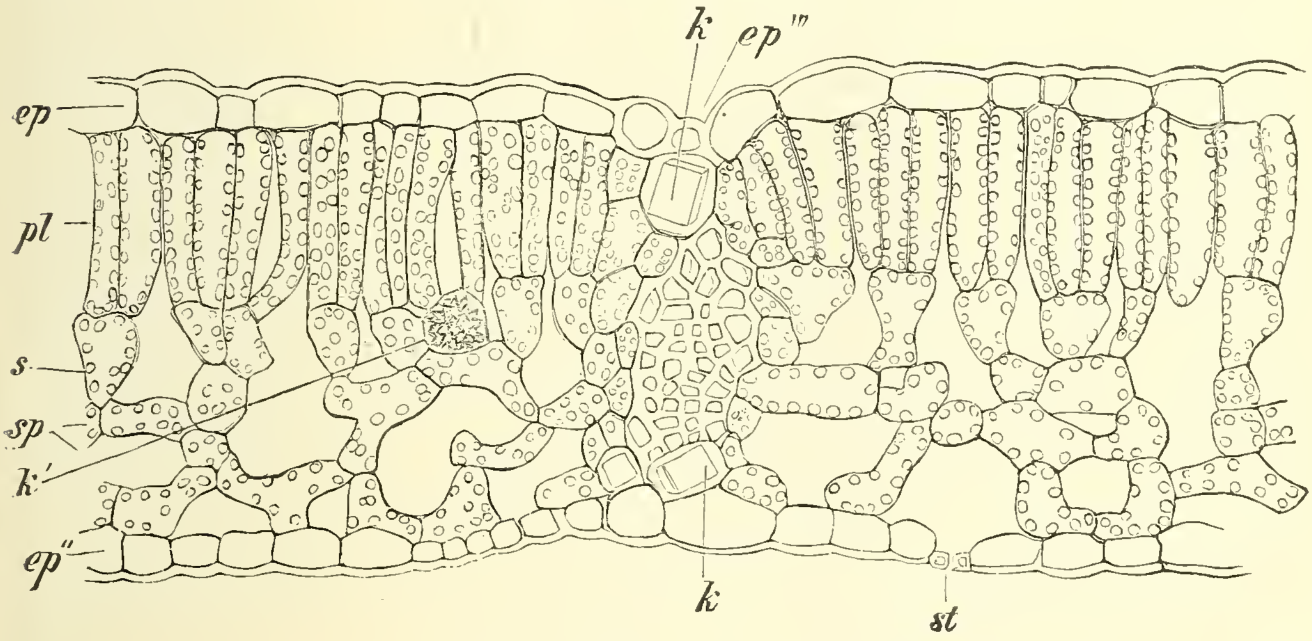


FIG. 132.—Transverse section of a leaf of *Fagus sylvatica*. *ep*, Epidermis of upper surface; *ep''*, epidermis of under surface; *ep'''*, elongated epidermal cell above a vascular bundle; *pl*, palisade parenchyma; *s*, collecting cells; *sp*, spongy parenchyma; *k*, idioblasts with crystals, in *k'* with crystal aggregate; *st*, stoma. (× 360.)

At the base of the lamina the tissues close together and pass into the leaf petiole. The dorsiventral structure of the leaf becomes less evident in the petiole; the cells become more elongated, either for the better performance of their conductive functions, or to enhance the mechanical rigidity of the tissue. In Angiosperms the partial cylinders of the leaf, usually an odd number, and each containing a single vascular bundle, arrange themselves in regular order as they pass through the petiole, and frequently form a bow-shaped figure, opening upwards. On entering the stem the vascular bundles of the leaf join the vascular bundles of the central cylinder; the fundamental tissue of the leaf-cylinders becomes, similarly, united with the corresponding tissue of the central cylinders. In the petioles of Ferns, the partial cylinders are accompanied, as in the stem, by sclerenchymatous fibres. It is the peculiar arrangement of these brown-walled sclerenchymatous plates which forms the double eagle apparent on cross-sections of the petiole of *Pteris aquilina*, and from which it derives its specific name.

In certain families of the Dicotyledons, particularly in the *Crassulaceae*, the mesophyll of the leaf-lamina forms peculiar masses of tissue called the EPITHEME between the swollen terminations of the bundles and the epidermis. The cells of the epitheme are small and, for the most part, devoid of chlorophyll; they are full of water, and joined closely together, leaving only very small interspaces, which are filled with water. The epithemes serve as internal hydathodes (cf. p. 102) for the discharge of water, in most cases by means of water-pores (p. 99) situated immediately over them.

The Course of Vascular Bundles (68).—The bundles maintain a definite course and arrangement within the body of a plant. It is sometimes possible, by maceration, to obtain preparations in which the course taken by the bundles may be followed. Similarly, by allowing a leaf, stem, or flower to lie in water until it has become softened and disintegrated, a skeleton formed by the more imperishable vascular system may be obtained.

Vascular bundles which pass from a leaf into a stem, and continue for a distance in a distinct course, are called LEAF-TRACES. The leaf-traces may be composed of one or more vascular bundles, and are accordingly distinguished as one-strand or many-strand leaf-traces. Sometimes a single vascular bundle becomes branched, and so appears to be composed of more than one bundle. Eventually, however, each bundle coalesces with another entering the stem from a lower leaf. The arrangement of the bundles in a stem varies according to the distance and direction traversed before the coalescence of the bundles takes place. A relatively simple bundle arrangement may be seen in the *Equisetaceae*. In this family the leaves are arranged in alternating whorls. From each leaf a one-strand leaf-trace enters the stem; at the next lower node each bundle bifurcates, and each half coalesces with the bundles entering the stem from the leaves of that node. This arrangement of the bundles may be shown diagrammatically, by representing the bundles as if on the surface of an unrolled cylinder, so that they all appear in one plane. This is shown in Fig. 133, and the connections of the bundles of the lateral branches with the bundles of the parent stem are also shown (*g*). As the branches, in the case of the *Equisetaceae*, alternate with the leaves, their bundles on entering the stem are between two leaf-traces of the same node, and at once become fused with the leaf-trace which has come from the leaf immediately above them in the next higher node. The arrangement of the bundles in the Yew (*Taxus baccata*), although its leaf-traces have only one bundle, is much more complicated (Fig. 134), for the bundles maintain a distinct course throughout twelve internodes before coalescing. Each bundle at first descends in a straight direction through four internodes; it then curves to the side to give place to a newly-entering leaf-trace, with which it finally coalesces at the twelfth internode. The position of a leaf necessarily determines the point of entrance of its leaf-trace into the stem, and accordingly a diagram (Fig. 134) of the bundles of *Taxus* will exhibit a divergence of the leaf-trace corresponding to the $\frac{5}{13}$ divergence of the leaves. The course taken by the leaf-traces in the stem, however, is independent of the leaf position, and varies considerably in different stems, although the divergence of their leaves may be the same.

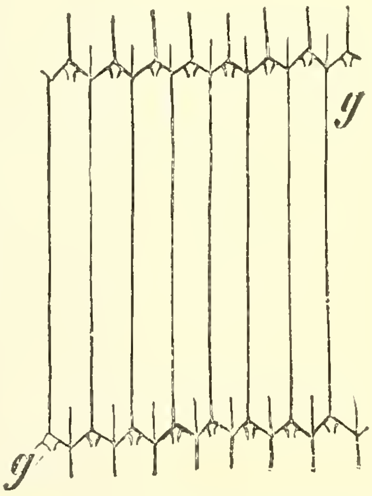


FIG. 133.—Diagram showing the course of the vascular bundles in the stem of *Equisetum arvense*. *g*, Fusion of vascular bundles of the lateral shoots with those of the parent shoot.

The traces of the axillary buds of most Gymnosperms and Dicotyledons tend to enter the shoot as two united strands which insert themselves on the corresponding leaf-trace.

As a general rule, the leaf-trace bundles in Gymnosperms and Dicotyledons arrange themselves in a circle in the stem. There are, however, Dicotyledons in which the vascular bundles form two (*Phytolacca dioica*, *Piper*) or more circles (*Amarantus*, *Papaver*, *Thalictrum*). In such cases the inner circle is usually more or less irregular.

In the stems of Monocotyledons (Fig. 126) the vascular bundles are scattered, and without any apparent regular order. Their irregular arrangement is due to the varying distances to which the bundles of the leaf-traces penetrate into the central cylinder of the stem. A common arrangement of the bundles in monocotyledonous stems is that of the so-called Palm type, in which each leaf-trace consists of the numerous bundles which pass singly into the stem from the broad leaf-base. The median bundle penetrates to the middle of the stem. The depth to which the lateral bundles penetrate varies with their remoteness from the median bundle. In their descending course the bundles gradually curve outwards, and finally join other bundles near the periphery of the stem. The number of internodes, therefore, through which a bundle passes before coalescence is variable; the median bundle, however, continues distinct for the longest distance. The deeper penetration and greater length of the median bundle become apparent in a median longitudinal section of such a stem (Fig. 135). The bundles entering the stem from axillary shoots pursue a similarly curved course to those entering from leaves.

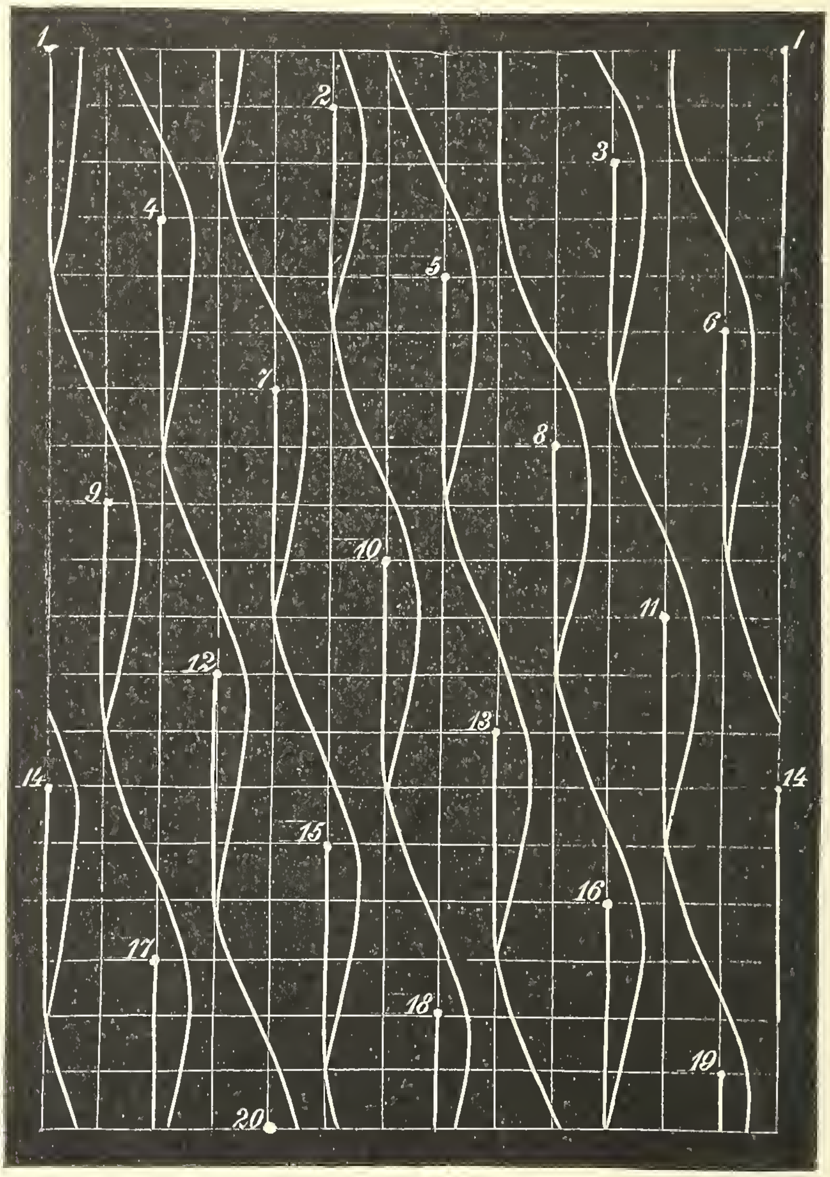


FIG. 134.—Diagram showing the course of the vascular bundles in a shoot of *Taxus baccata*.

In addition to the leaf-trace bundles or COMMON BUNDLES, which are common to both leaf and stem, there are others, called CAULINE BUNDLES, which belong solely to the stem, and again others, FOLIAR BUNDLES, which, on entering the stem from the leaf, at once coalesce with other bundles and have no independent existence in the stem. The bundles of the Pteridophytes are continued as cauline bundles in the stem, and those from the leaves join on to the bundles of the stem.

The stems of many Dicotyledons (*Begonia*, *Aralia*) in addition to leaf-traces possess cauline bundles, which are situated in the pith within the ring of leaf-trace bundles of the internodes; while the arrangement of the bundles at the nodes is more complicated, as the cauline bundles then branch and are connected with the leaf-traces.

Within the central cylinder of roots, the xylem and phloem strands pursue their vertical direction without deviation. If the changes occurring in the arrangement of the vascular bundles, during their passage from the hypocotyl (p. 49) into the root, be followed in a seedling, it will be found that the xylem and phloem portions of collateral bundles separate from one another, and at the same time the xylem portions twist through an angle of 180°, so that their inner sides become turned outwards. The separation of the xylem and phloem may be accomplished without any further division of the bundles, the xylem and phloem portions of which then simply arrange themselves side by side; or it may be accompanied by a complete radial division of the phloem, and a subsequent coalescence between the parts of the phloem of different bundles.

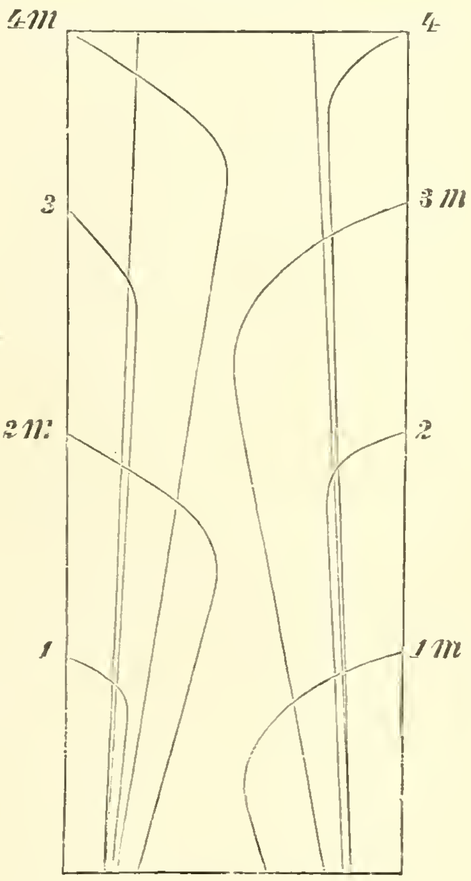


Fig. 135.—Diagram showing the course of the vascular bundles of Monocotyledons of the Palm type, with alternating, two-ranked amplexicaul leaves. The numbers indicate the sequence of the leaves; *m*, median bundle. (After De Bary.)

A Special Form of Growth in Thickness of the Stem by means of the Continued Enlargement of the Fundamental Tissue.—This is often exhibited by Palms. Eichler ([69]) has shown that the growth in thickness is solely due to the continued expansion of the already existing cells of the fundamental tissue of the central cylinder. In this process, by the expansion of the cell lumen and increased thickening of the walls, the strands of sclerenchymatous fibres accompanying the vascular bundles on their phloem sides also become greatly enlarged. In this form of growth in thickness no new elements are formed.

Enlargement due to Continued Cell Divisions in the Fundamental Tissue.—This is seen most strikingly in the growth of the fruits of many Angiosperms. In their development from the small rudiment in the flower there may be a great increase in size, although no new meristematic tissue has been formed. The growth is due to repeated divisions in the epidermal cells and in those of the fundamental tissue. The tissue thus produced may when mature be then walled, or its cells may undergo various changes in form and in the thickness of their walls.

The Secondary Tissues (70)

Through the activity of a cambial tissue, functioning either as a primary or secondary meristem (p. 95), secondary tissues are added to the previously existing primary tissues, or even substituted for them. Although, phylogenetically considered, secondary tissues seem to have been developed first in the Pteridophytes in forms now only known in a fossil condition, *Calamarieae*, *Sigillarieae*, *Lepidodendra*, they are now only of general occurrence in the Phanerogams, and in them the formation of secondary tissues is almost exclusively confined to the roots and stems.

Growth in Thickness of the Stem in Gymnosperms and Dicotyledons.—The cambium of the open vascular bundles of Gymnosperms and Dicotyledons, which exhibit a growth in thickness, commences its activity almost directly after the formation of the primary tissue. The cambium or primary meristem remaining between the xylem and phloem portions of the bundles consists of only a few layers of thin-walled cells full of protoplasm. Of these cambial layers the middle one is termed the INITIAL LAYER; and from it proceeds the development of new tissue elements. Its activity consists in a continued division by means of tangential and occasionally radial walls. The new cells thus continuously given off toward the xylem and phloem sides of the bundles experience another tangential division before attaining their definite form as elements of the xylem or phloem portions. The vascular bundles of Gymnosperms and Dicotyledons capable of secondary growth are usually arranged in a circle. After the cambium in the bundles begins its activity, a zone of tangentially dividing tissue, called the INTERFASCICULAR CAMBIUM, develops in the primary medullary rays between the original bundles, and, uniting with the cambium in the bundles, forms a complete cambium ring. This cambium ring is thus composed of two distinct forms of meristematic tissue; for while the cambium of the bundles or the FASCICULAR CAMBIUM consists of primary meristem (p. 95), the connecting zone of inter-

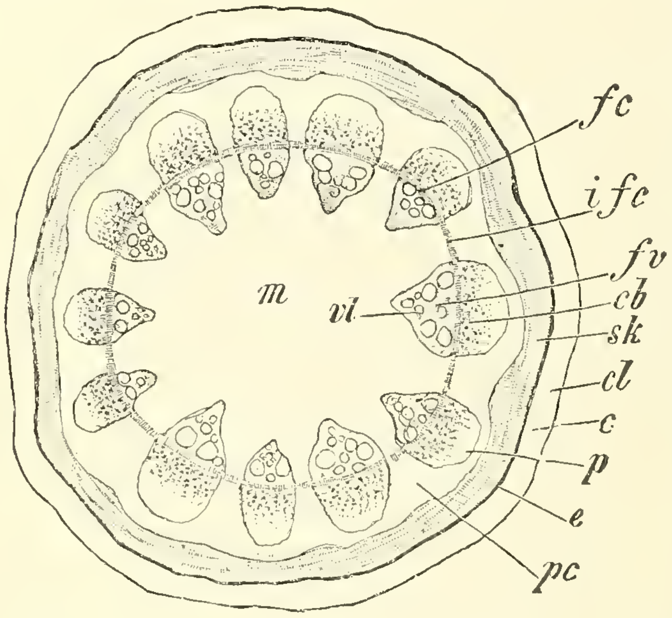


FIG. 136.—Transverse section of a stem of *Aristolochia Sipho* 5 mm. in thickness. *m*, Medulla; *fv*, vascular bundle; *vl*, xylem; *cb*, phloem; *fc*, fascicular cambium; *ifc*, interfascicular cambium; *p*, phloem parenchyma; *pc*, pericycle; *sk*, ring of sclerenchyma; *e*, starch-sheath; *c*, primary cortex; *cl*, collenchyma in primary cortex. (× 9.)

fascicular cambium is of later development, and is consequently a secondary meristem (p. 95). A cross-section of a young stem of *Aristolochia Sipho*, with the cambium ring in process of formation, is represented in Fig. 136; in Fig. 137 a single bundle of

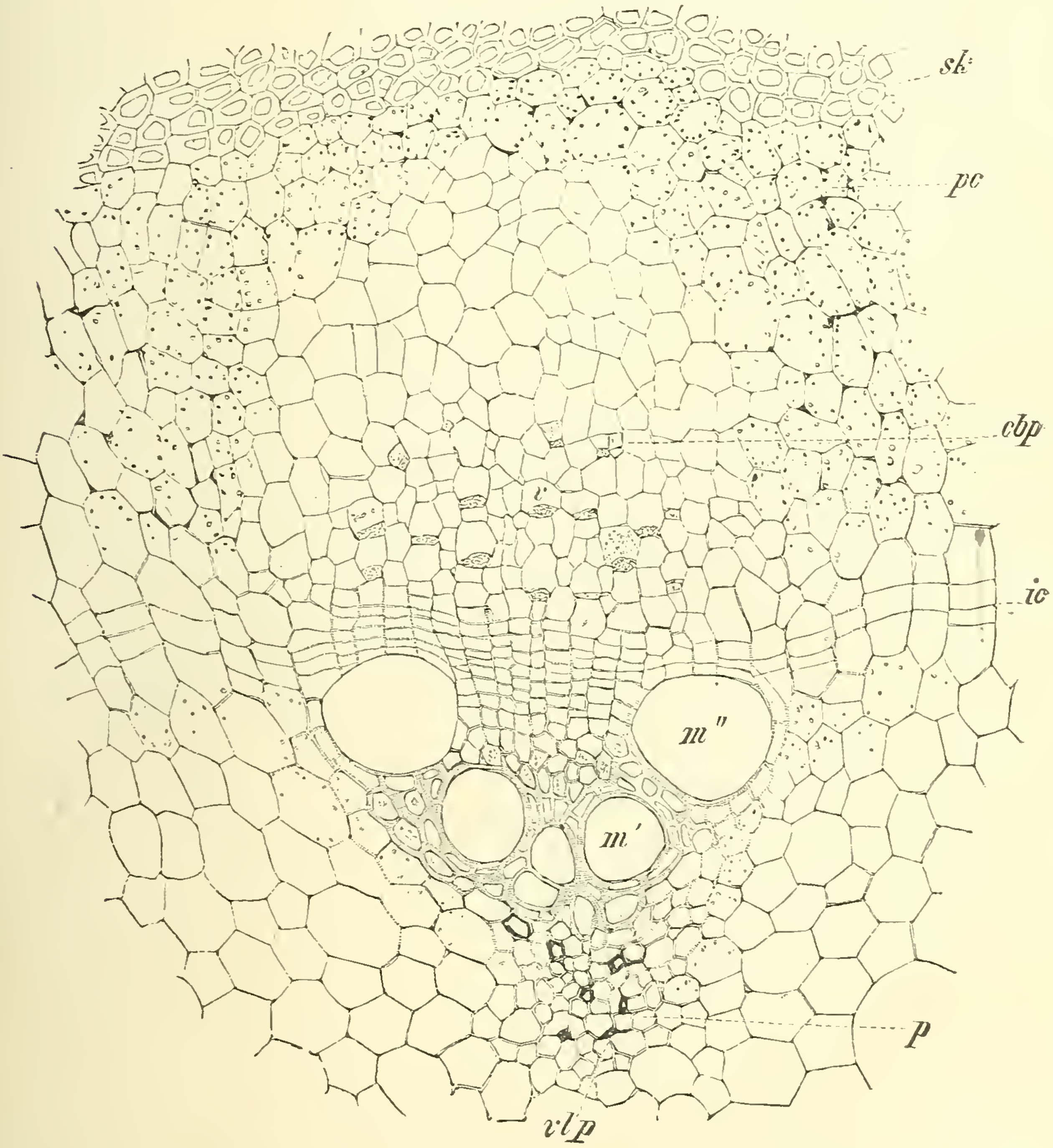


FIG. 137.—Transverse section of a stem of *Aristolochia Sipho* in the first year of its growth, showing a vascular bundle with cambium in active division. *p*, Vascular parenchyma; *vlp*, protoxylem; *m'* and *m''*, vessels with bordered pits; *ic*, interfascicular cambium in continuation with the fascicular cambium; *v*, sieve-tubes; *cbp*, protophloem; *pc*, pericycle; *sk*, inner part of ring of sclerenchymatous fibres. (× 130.)

the same cross-section, more highly magnified, shows the fascicular cambium in a condition of active division. Within the bundle may be seen two large vessels (*m''*), in a still incomplete state; while in the adjoining fundamental tissue the cells which give rise to the interfascicular cambium may be plainly distinguished. All the tissue arising from the inner side of the cambium ring goes to form the WOOD, while that produced on the outside is termed BAST. The vascular portions of the wood form the WOOD STRANDS, the sieve portions within the bast the BAST STRANDS. By the activity of the interfascicular cambium, the primary medullary rays are continued throughout both the wood and bast. As the wood and bast strands enlarge, SECONDARY MEDULLARY RAYS are developed from the fascicular cambium. In one direction the secondary medullary rays terminate blindly in the wood, and in the other in the bast; the later they develop, the less deeply they penetrate the tissues on either side of the cambium.

The primary medullary rays are therefore often distinguished as long, the secondary as short medullary rays. The expression transverse parenchyma is also

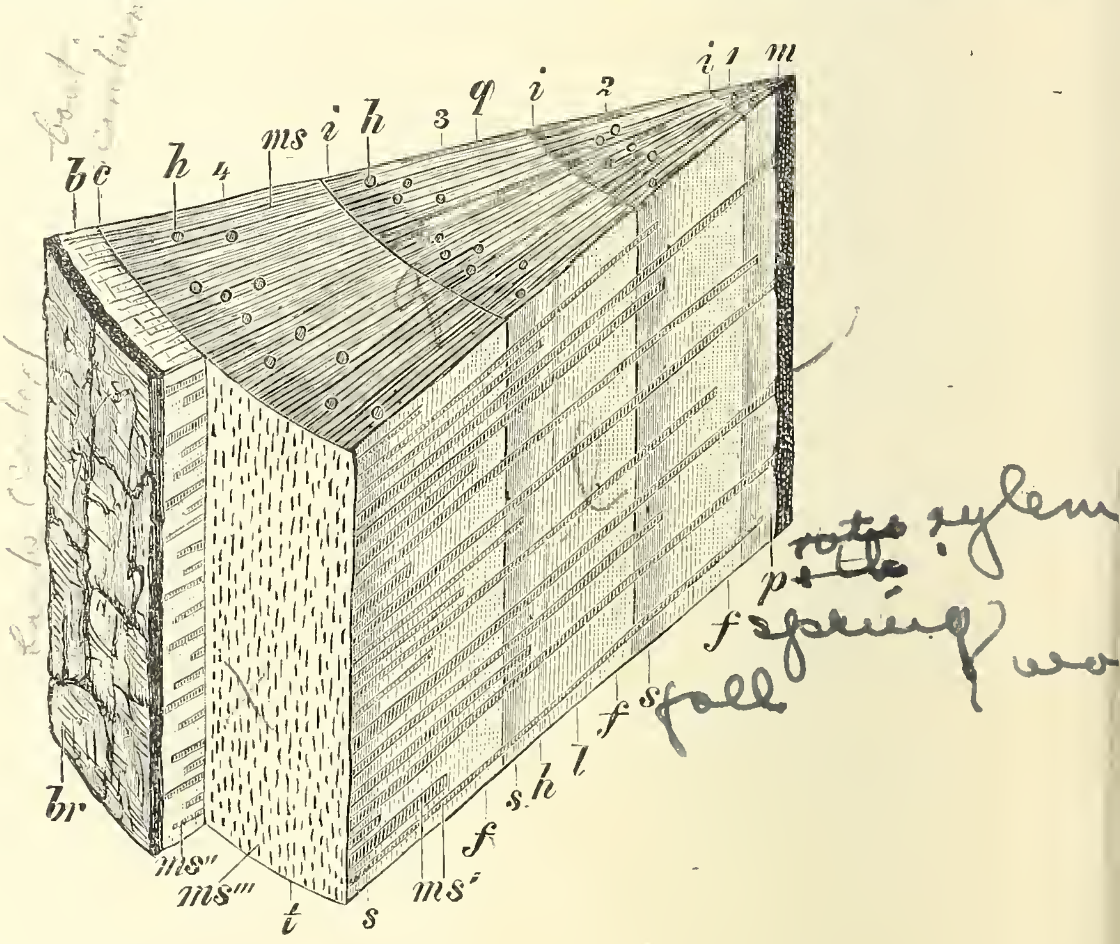


FIG. 138.—Portion of a four-year-old stem of the Pine, *Pinus sylvestris*, cut in winter. *q*, Transverse view; *l*, radial view; *t*, tangential view; *f*, early wood; *s*, late wood; *m*, medulla; *p*, protoxylem; 1, 2, 3, 4, the four successive annual rings of the wood; *i*, junction of the wood of successive years; *ms*, *ms'*, *ms'''*, medullary rays in transverse, radial, and tangential view; *ms''*, radial view of medullary rays in the bast; *c*, cambium-ring; *b*, bast; *h*, resin canals; *br*, bark external to the first periderm layer, corresponding to the primary cortex. (× 6.)

sometimes used to designate the medullary rays, which in fact are composed almost exclusively of parenchymatous tissue. The cells given off by the initial layer of the cambium for the formation of medullary rays do not undergo a further division, as in other cases, but assume at once the character of medullary ray cells.

The cambium cells have, for the most part, the shape of right-angled prisms, of which the radial diameter is smaller than the tangential. The ends of these prisms are usually one-sided, tapering to a point, alternately on the right and left sides. The length of the cambium cells varies in different plants, but those from which medullary rays are formed are the shorter. The primary vascular portions of the bundles projecting into the medulla constitute what is known as the MEDULLARY SHEATH.

Owing to climatic variations, the cambium tissue of woody plants exhibits a periodical activity which results in the formation of ANNUAL RINGS of growth (Figs. 138, 140, 146). In spring, during the period of energetic growth, larger tracheal elements are developed than in the following seasons (Figs. 140, 148). For this reason a difference is perceptible between the EARLY WOOD (spring wood), which is composed of large elements especially active in the conveyance of water (Fig. 140, *f*), and the LATE WOOD (autumn wood), consisting of narrow elements which impart to a stem its necessary rigidity (Fig. 140, *s*). Throughout the greater part of the temperate zone, the formation of wood ceases in the latter part of August, until the following spring, when the larger elements of the spring wood are again developed. Through the consequent contrast in the structure of the early and the late wood, the limits (Fig. 138, *i*) between successive annual rings of growth become so sharply defined as to be visible even to the naked eye, and so serve as a means of computing the age of a plant.

Under certain conditions the number of annual rings may exceed the number of years of growth, as, for instance, when MIDSUMMER GROWTH occurs, such as commonly happens in the Oak, when, after the destruction of leaves by caterpillars, a second formation of spring wood is occasioned by the new outgrowths thus induced. In the wood of tropical plants the annual rings may be entirely absent. This occurs, for example, in the tropical Conifers of the genus *Araucaria*, which, in this respect, show a marked contrast to the Conifers of the northern zone. Any interruption of growth, such as would occur during a drought, followed by a period of renewed activity, may occasion the formation of annual rings even in tropical plants.

Although a cessation in the formation of wood takes place so early, the cambium tissue continues to form bast so long as climatic conditions permit. As a rule, however, fewer elements are added to the bast than to the wood. Up to a certain period, in the age of woody plants, the elements of both wood and bast exhibit a progressive increase in size.

The living elements may remain in a state of greater or less activity throughout the whole of the wood, extending even to the pith; such wood is called splint wood: the Beech (*Fagus sylvatica*) may be quoted as an example; in other trees which form heart-wood, the living elements die after a certain time, so that only dead tissues are found at a certain distance from the cambium. Before the death of the living cells, they usually produce certain substances, such as tannin and gums, which penetrate the cell walls of the surrounding elements, and also partially close their cavities. The tannins impart to the dead wood a distinct colour, often very characteristic, especially when it has been transformed into wood dyes, or so-called XYLOCHROME. The tannin in the woody walls acts as a preservative against decay, while the gums close the functionless water-courses of the dead wood. The dead portion of the wood of a stem is called the HEART-WOOD or DURAMEN, in contrast to the living SAP-WOOD or ALBURNUM. Usually the splint or sap-wood is at once distinguishable from the heart-wood by its lighter colour. In some stems, however, the heart-wood does not change its colour. In that case, as the protecting materials are generally absent, it is liable to decay, and then, as so often occurs in the willow, the stem becomes hollow.

The sap-wood is limited, according to the kind of wood, to a larger or smaller number of the younger annual rings, and to it falls the task of water conduction. The distinction between sap- and heart-wood is sharpest where the latter is dark-coloured, as in the Oak, with its brown heart-wood, and in species of *Diospyros*, whose black heart-wood furnishes ebony. The darker the heart-wood, the harder and more durable it usually is. The following may be mentioned as examples of woods which yield dyes and colouring principles—*Haematoxylon campechianum*, L. (Campeachy wood, logwood), with a blue heart-wood from which HÆMATOXYLIN is extracted ; *Pterocarpus santalinus*, L. fil. (red sandalwood), from the heart-wood of which SANTALIN is obtained ; *Caesalpinia brasiliensis*, L., and *C. echinata*, Lam. (Brazil wood, Pernambuco wood), with a red heart-wood which supplies BRASILIN ; and the Alsage Orange, *Maclura aurantiaca*, Nutt. (yellow Brazil wood), which has a yellow heart-wood from which MORIN is derived. Inorganic substances may also be deposited in the duramen ; thus calcium carbonate is found especially in the vessels of the Elm and the Beech, while silicic acid occurs in those of the Teak (*Tectona grandis*).

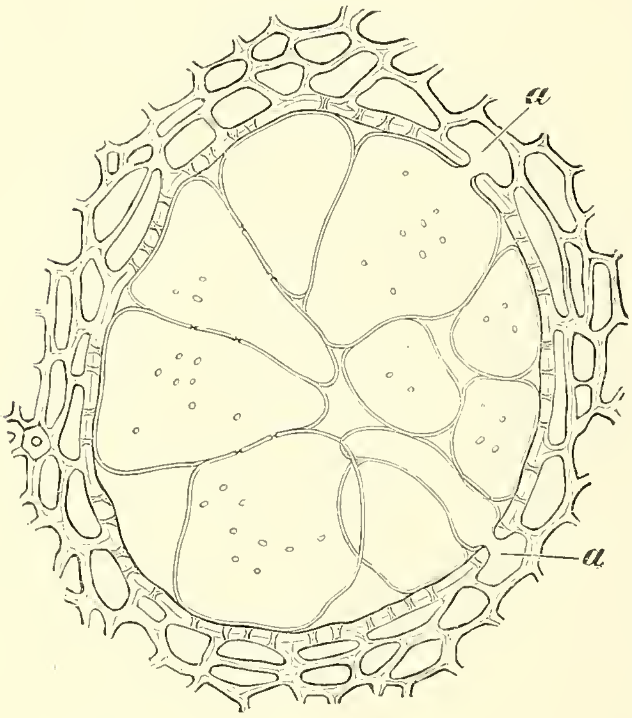


FIG. 139.—Transverse section of a vessel from the heart-wood of *Robinia Pseudacacia*, closed by tyloses ; at *a*, *a* is shown the connection between the tyloses and the cells from which they have been formed. (× 300.)

TYLOSES (Fig. 139) are also instrumental in closing the water-courses of the heart-wood. These are intrusive growths from living cells, which penetrate the cavities of the adjoining tracheal elements during the transition of the sap-wood into heart-wood. In the formation of tyloses the closing membrane of the pits of pitted vessels forms bulging ingrowths into the vessel cavities. Such bulging ingrowths increase in size until several meet, and so more or less completely close the cavities of the vessels into which they have intruded. The closing membrane of the bordered pits in the heart-wood is pushed to one side, so that the torus presses against the opening of the pit and completely closes it. According to H. MAYR (71), resin does not penetrate the walls of wood cells under normal conditions ; the wood of Conifers only becomes resinous through the impregnation of the cell walls with resin, after they have become dried up through wounds or other causes. The resin-ducts of Conifers may also be closed by the formation of tyloses.

The **elements of secondary growth** in Gymnosperms and Dicotyledons differ. The vascular strands of Gymnosperms are composed almost exclusively of tracheids (Fig. 140). These are provided with bordered pits which are situated, for the most part, in their radial walls. The tracheids of the spring-wood (*f*) have larger cavities than those formed later (*s*). Parenchyma is also present in the wood, though in relatively small amount; in some *Abietineae* resin-passages occur in it (Fig. 138, *h*).

With the exception of the *Gnetaceae*, true vessels are not found in the secondary growth, nor in the primary vascular portions, of the bundles of Gymnosperms. The wood produced by the cambium consists of radial rows of tracheids, the number of which is occasionally doubled by the radial division of a cambium cell (Fig. 140, *a*).

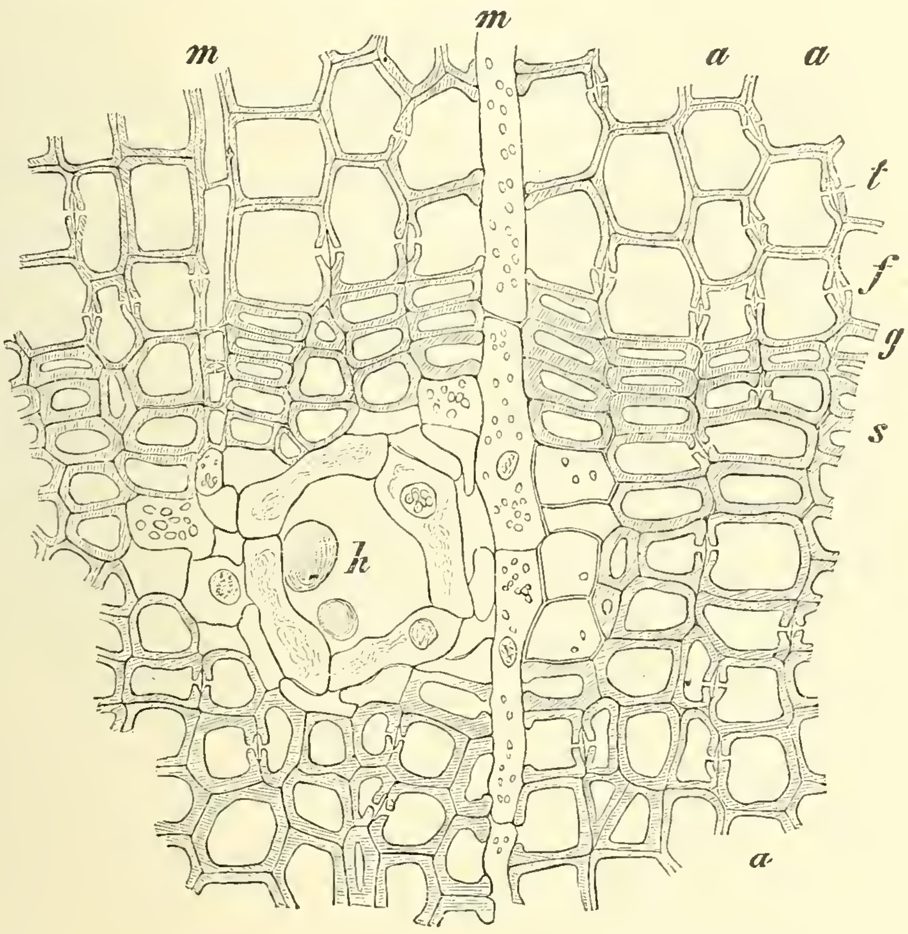


FIG. 140.—Transverse section of the wood of a Pine at the junction of two annual rings. *f*, Early wood; *s*, late wood; *t*, bordered pit; *a*, interposition of a new row of tracheids resulting from the radial division of a cambium cell; *h*, resin canals; *m*, medullary rays; *g*, limit of late wood. (× 240.)

The tracheids are often over a millimetre long, much longer than the cambium cells from which they are developed. They attain this length by a subsequent growth, during which their growing ends become pushed in between one another.

In addition to the tracheids, small amounts of wood parenchyma are also produced in Gymnosperms by a transverse division of the cambium cells. It is in the parenchymatous cell rows of the wood of Pines, Spruce-Firs, and Larches that the schizogenous resin-ducts are produced (Fig. 140, *h*). In other Conifers the wood parenchyma consists of simple rows of cells, which afterwards become filled with resin.

Besides tracheids (*t*) and wood parenchyma (*hp*), other elements take part in the composition of the secondary wood of a Dicotyledon; these are the vessels (tracheæ, *g*), and the wood fibres (*h*) (Figs. 144, 145). The cells of the wood parenchyma are short and have abundant contents, the wood fibres are thick-walled long cells with pointed ends. The elements with wider lumens, especially the vessels, are abundant in the spring-wood, in which water conduction is important. The autumn-wood, on the other hand, consists of narrow elements, among which the wood fibres, which contribute to the rigidity of the plant, are numerous. On account of these differences between spring and autumn-wood the annual rings are well marked (Fig. 148).

All the elements entering into the formation of the wood of Dicotyledons can be derived from the two classes of tissue already met with in the Gymnosperms, the tracheal tissue and the parenchymatous tissue of the wood. The tracheids and vessels belong to the former class, while under the parenchymatous tissue are included the wood parenchyma, fibrous cells of greater length but with similar contents (Fig. 145, *ef*), and the wood fibres.

The tracheal tissue consists of elements which lose their living contents at an early stage, and in their fully-developed condition are in reality only dead cell cavities. In this class are included TRACHEIDS having relatively wide lumina and large bordered pits (Fig. 144, *t*), and often also spirally thickened tracheids which serve as water-carriers; VASCULAR TRACHEIDS (*gt*), with similar functions, but with the structure and thickening of vessels; FIBRE TRACHEIDS (*ft*), with small lumina and pointed ends, having only small, obliquely elongated bordered pits, and, in extreme cases, exercising merely mechanical functions; and finally TRACHEÆ (*g*), formed by cell fusion, and provided with all the different forms of thickenings by which they are distinguished as annular, spiral, reticulate, or pitted vessels. All vessels function as water-carriers. If they have small lumina and resemble tracheids, they may be distinguished as TRACHEIDAL VESSELS (*lg*); if, as is generally the case, they have bordered pits on their lateral walls, they are usually provided with tertiary thickening layers in the form of thin spiral bands (Fig. 149, *m*). In the parenchymatous tissue of the wood, the cells (Fig. 145) generally retain their living contents, and never develop true bordered pits with a torus in the closing membrane, which are so characteristic of the water-conducting elements. All tissues of this class may be best derived from wood parenchyma. The wood parenchyma is produced by transverse divisions of the cambium cells, and accordingly consists of rows of cells (*hp*) with transverse division walls, and others obliquely disposed, which correspond to the alternately differently pointed ends of the cambium mother cells.

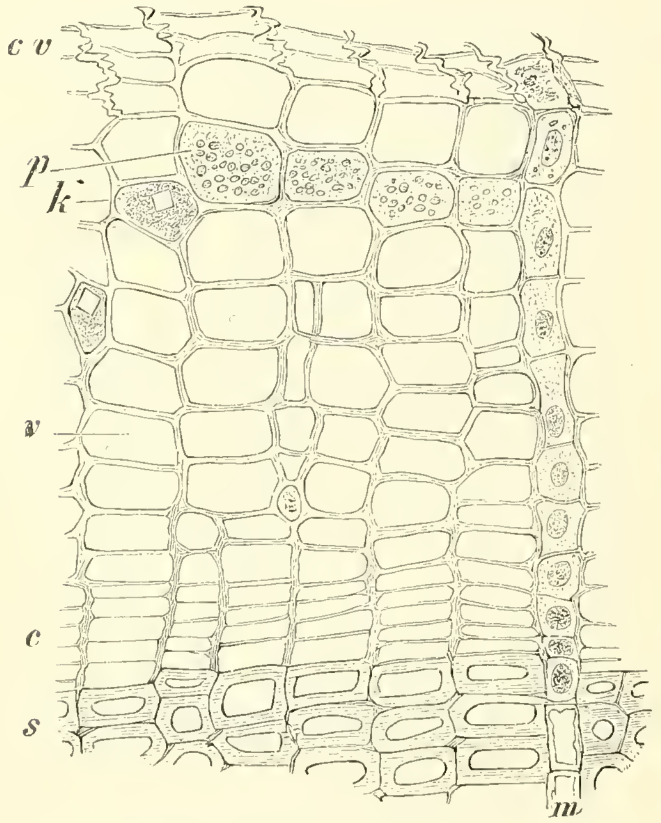


FIG. 141.—Part of a transverse section of the stem of a Pine. *s*, Late wood; *c*, cambium; *v*, sieve-tubes; *p*, bast parenchyma; *k*, cell of bast parenchyma containing crystal; *cv*, sieve-tubes, compressed and functionless; *m*, medullary ray. (× 240.)

The cells of the wood parenchyma are provided with simple round or elliptical pits, varying in size in different kinds of wood; they generally contain starch; and some of them also take up by-products, resulting from metabolism, or from the chemical changes taking place within a plant in the processes of its nutrition and growth. The cells having the closest resemblance to those of typical wood parenchyma are the so-called FIBROUS CELLS (*cf*). In their contents, as well as in their wall thickenings, they are similar to the cells of wood parenchyma, but are formed directly from one entire cambium cell. In their formation, the cells of the cambium tissue do not undergo a transverse division, but become more or less elongated and fibrous. The LIBRIFORM FIBRES or WOOD FIBRES (*h*) have a similar origin, but are even more elongated and have thicker walls, and, at the same time, narrow, obliquely elongated, simple pits. Although the wood fibres may continue living, in the more extremely developed forms (*h*) they lose their living contents. They are then filled with air, and their function is merely mechanical. Under certain conditions, by later transverse divisions, the libriform fibres may become transformed into SEPTATE WOOD FIBRES (*gh*). The transverse septa thus formed remain thin, and form a striking contrast to the more strongly thickened lateral walls. While the tracheal tissues are engaged in providing for the conduction of water, the duty of conducting and storing the products of assimilation, in particular the carbohydrates, is performed by the parenchymatous tissues of the wood. Both forms of tissue, however, aid in maintaining the rigidity and elasticity of the plant body, and, in their most extreme development, furnish such elements as the fibre

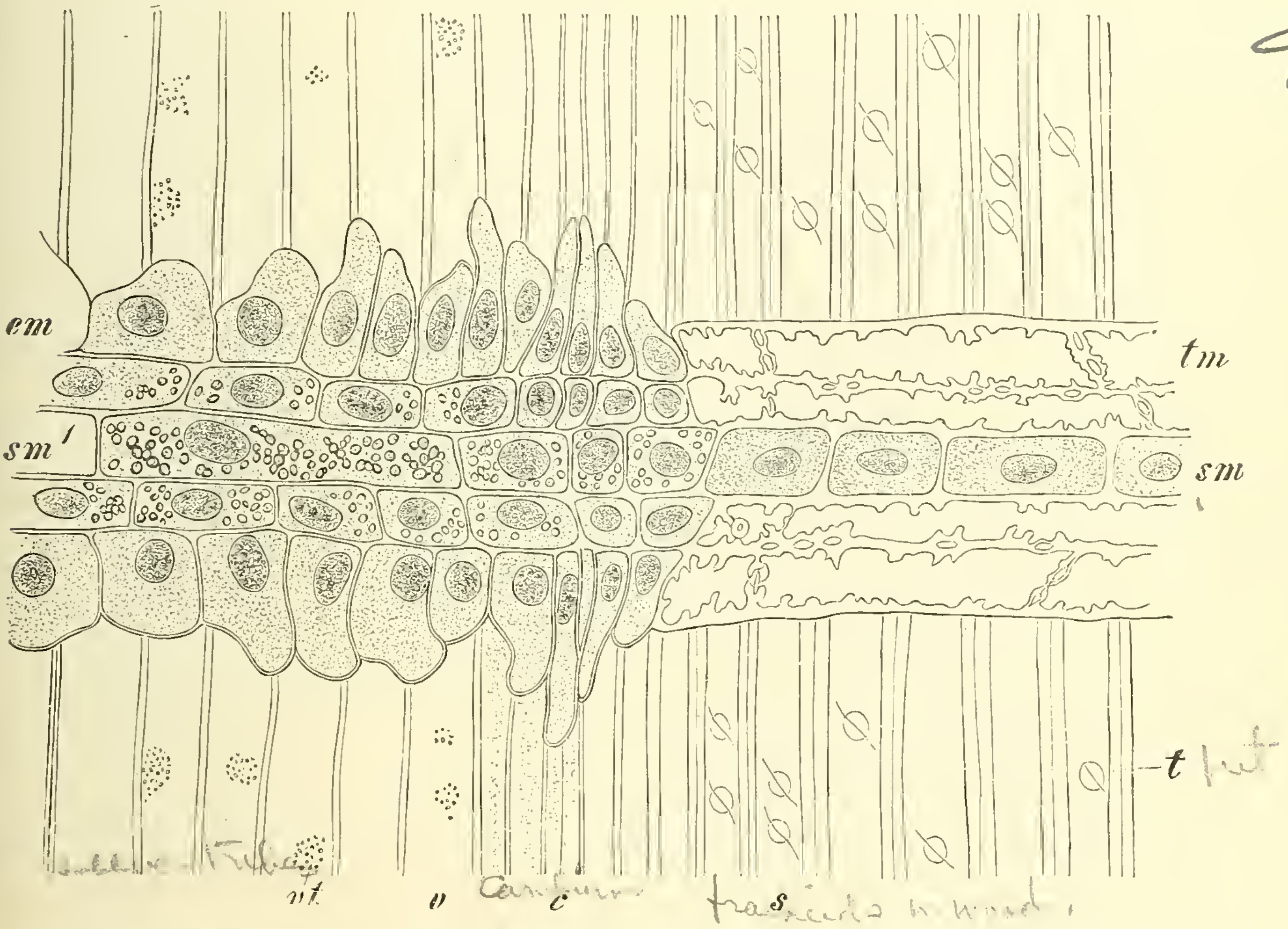


FIG. 142.—Radial section of a Pine stem, at the junction of the wood and bast. *s*, Late tracheids; *t*, bordered pits; *c*, cambium; *v*, sieve-tubes; *vt*, sieve-pits; *tm*, tracheidal medullary ray cells; *sm*, medullary ray cells in the wood, containing starch; *sm'*, the same, in the bast; *em*, medullary ray cells, with albuminous contents. (× 240.)

tracheids on the one hand, and on the other the empty wood fibres, which are only capable of performing mechanical functions.

The wood of Dicotyledons is made up of the elements of these two classes of tissue, the tracheal and the parenchymatous, but all the different elements are not necessarily represented in any one kind of wood.

Drimys, a genus closely allied to the Magnolias, is the only Dicotyledon of which the wood is formed solely of tracheids. This Dicotyledon closely resembles the Conifers in structure. In numerous *Leguminosae*, Willows, Poplars, and species of *Ficus*, on the other hand, the tracheal tissues are only represented by vessels, which perform the task of water conduction. In the wood strands of these plants there are also present wood parenchyma and a large amount of wood fibres, which contain only air. The vessels in climbing plants (lianes) are especially wide.

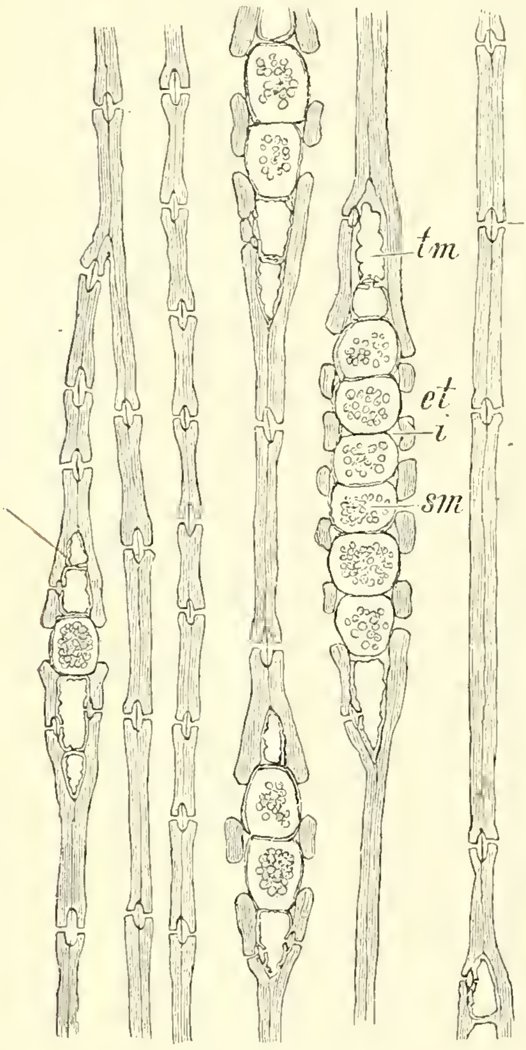


FIG. 143.—Tangential section of the late wood of a Pine. *t*, Bordered pit; *tm*, tracheidal medullary ray cells; *sm*, medullary ray cells containing starch; *et*, pit bordered only on one side; *i*, intercellular space in the medullary ray. (× 240.)

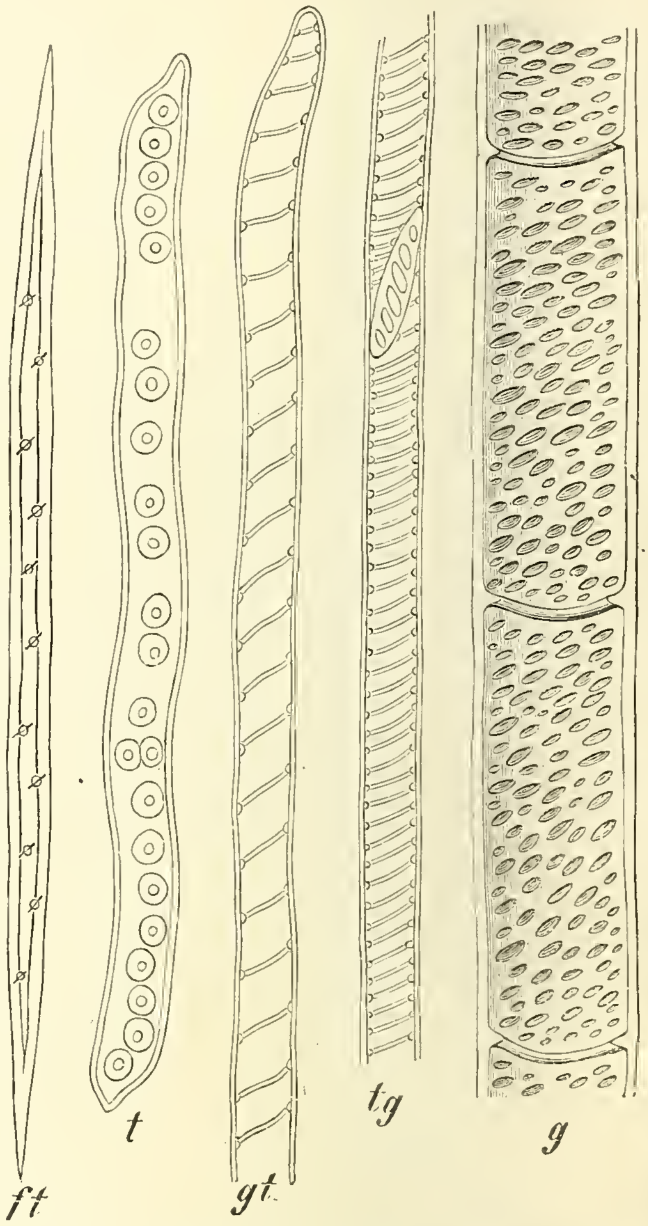


FIG. 144.—Elements of the tracheal tissue of the wood; diagrammatic. (For description, see text.)

The distribution of the living elements in the wood strands always bears a distinct relation to the water-courses which they accompany, enclosing them in a more or less complete sheath. The living cells adjoining the tracheal elements are in communication with them by means of one-sided bordered pits. When such pits occur in living cells the pit cavities are absent, but present in the case of tracheal elements ; they differ from the true bordered pits in the absence of a torus on the pit-closing membrane, and in being unlignified.

The Elements of the Secondary Phloem in Gymnosperms and woody Dicotyledons are sieve-tubes and companion cells, bast parenchyma with abundant cell contents, and long narrow bast fibres with strongly thickened walls. The sieve-tubes serve to conduct proteid materials; storage and conduction of carbohydrates take place in the parenchyma in which by-products of metabolism, such as tannins and calcium oxalate, also accumulate.

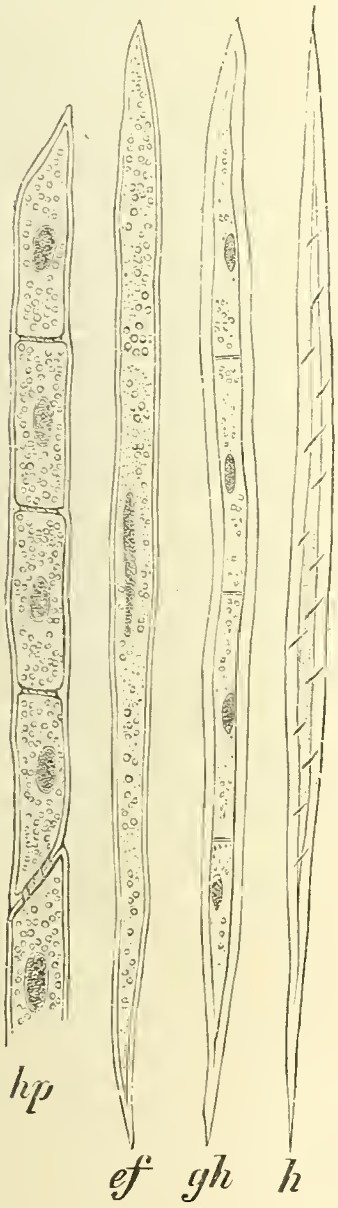


FIG. 145.—Elements of the parenchymatous tissue of the wood ; diagrammatic. (For description, see text.)

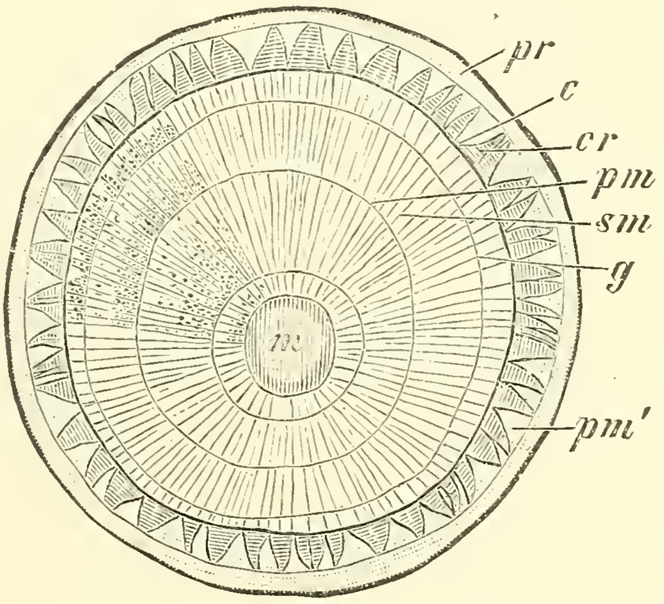


FIG. 146.—Transverse section of a stem of *Tilia parvifolia*, in the fourth year of its growth. *pr*, Primary cortex ; *c*, cambium ring ; *cr*, bast ; *pm*, primary medullary ray ; *pm'*, expanded extremity of a primary medullary ray ; *sm*, secondary medullary ray ; *g*, limit of third year's wood. (× 6.)

As in the case of the wood, the elements of the bast may be referred to two forms of tissue, the sieve-tube and the parenchymatous. The former is represented by the sieve-tubes or by these together with companion cells, the parenchymatous portion by the phloem parenchyma and the bast fibres, between which there are intermediate forms of element.

In the bast strands of Gymnosperms, the phloem elements produced by the cambium (Fig. 141, *c*) consist solely of sieve-tubes, the parenchymatous cells of the bast parenchyma (*p* and *k*), and, in certain cases, of bast fibres. These elements of the bast generally form alternating bands.

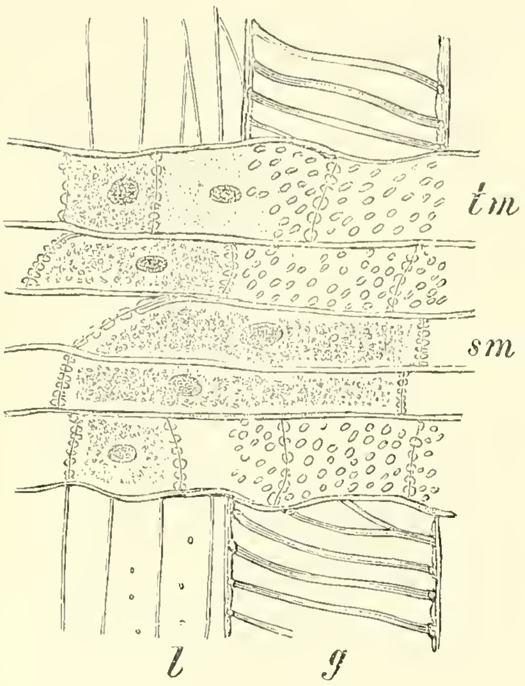


Fig. 147.—A radial section of the wood of *Tilia parvifolia*, showing a small medullary ray. *g*, Vessel; *l*, wood fibres; *tm*, medullary ray cells in communication with the water-courses by means of pits; *sm*, conducting cells of the medullary ray. (× 240.)

The *Araucarieae*, *Taxineae*, and some of the *Cupressineae* exhibit definite, vertical rows of bast parenchyma cells which are characterised by their abundant albuminous contents. These cells stand in close relation to the sieve-tubes and take the place of companion cells, which are not found in Gymnosperms. At a certain distance from the cambium the sieve-pits, both terminal and lateral, become over-laid by callus plates. During the vegetative period following their development, the sieve-tubes become empty and compressed together (Fig. 141, *cv*). The rows of bast parenchyma cells containing albuminous substances, which are found in some Conifers, undergo disorganisation at the same time as the adjacent sieve-tubes; the bast parenchyma cells which contain starch, on the other hand, continue living for years, and even increase in size, while the sieve-tubes become disorganised.

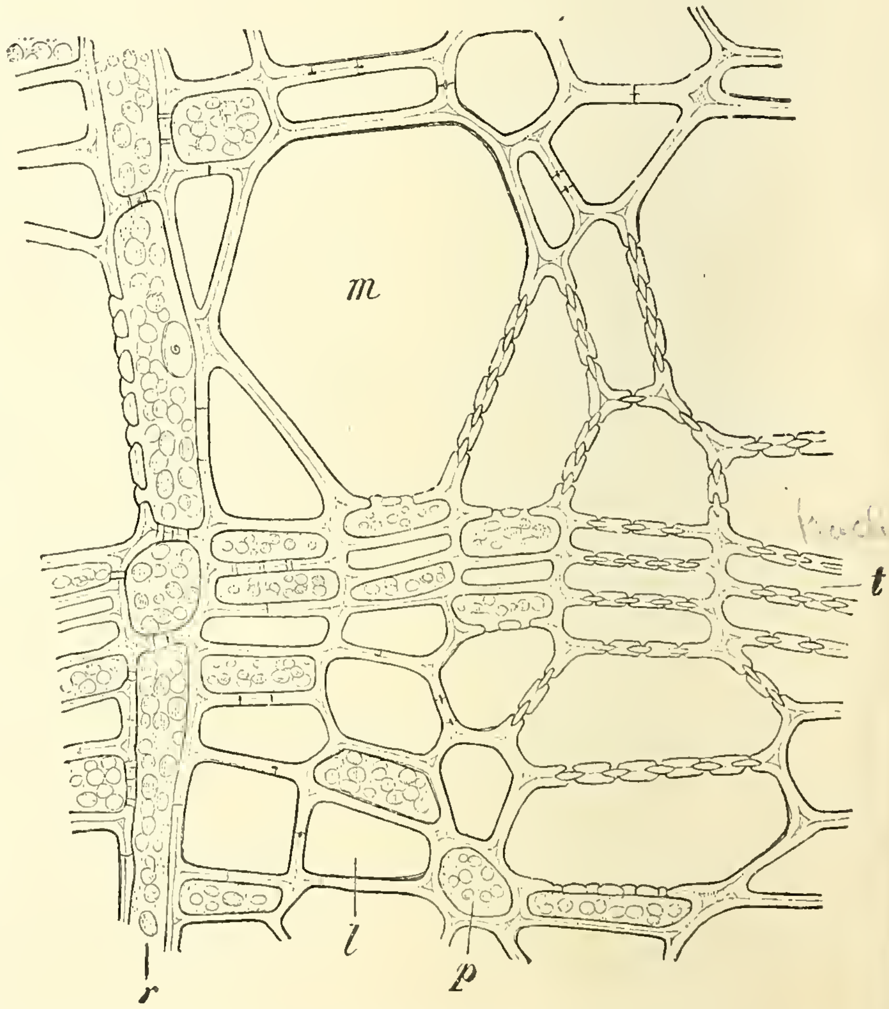


Fig. 148.—Portion of a transverse section of the wood of *Tilia parvifolia*. *m*, Large pitted vessel; *t*, tracheids; *l*, wood fibre; *p*, wood parenchyma; *r*, medullary ray. (× 540.)

The elements of the phloem tissue included in the bast strands of woody Dicotyledons (Fig. 150) are represented by SIEVE-TUBES (*v*) and COMPANION CELLS (*c*). To the parenchymatous tissues of the bast belong BAST PARENCHYMA (*p*), BAST FIBRES (*l*), and transitional forms between them.

The bast fibres, like the fibres of the wood, may occur in an unthickened form as FIBROUS CELLS, either with or without living contents, or they may be filled with starch, and finally may become septate.

An example of bast with an especially regular arrangement is afforded by the Lime (Fig. 150). In a cross-section, even under a low magnifying power, an alternation of shining white and dark-coloured tangential bands is noticeable. When more highly magnified, it can be readily seen that the white bands consist of strongly thickened bast fibres (Fig. 150, *l*). Adjoining them, there follow, towards the periphery, one layer of bast parenchyma cells (*p*), then a zone of wide sieve-tubes (*v*) and small companion cells (*c*); next to these come two layers of bast parenchyma (*p*), abundantly supplied with starch, and followed by a single interrupted layer of bast parenchyma cells containing crystals (*k*), and finally, another band of bast fibres (*l*). The farther removed the sieve-tubes and companion cells are from the cambium, the more crushed they become, until ultimately they appear as a compressed mass of cell walls without cell cavities. The starch-containing parenchyma, on the other hand, may remain for years unaltered. The differences in the appearance of the bast of dicotyledonous trees is due to the greater or less diameter of the sieve-tubes, the presence or absence of bast fibres, and the arrangement of the various elements.

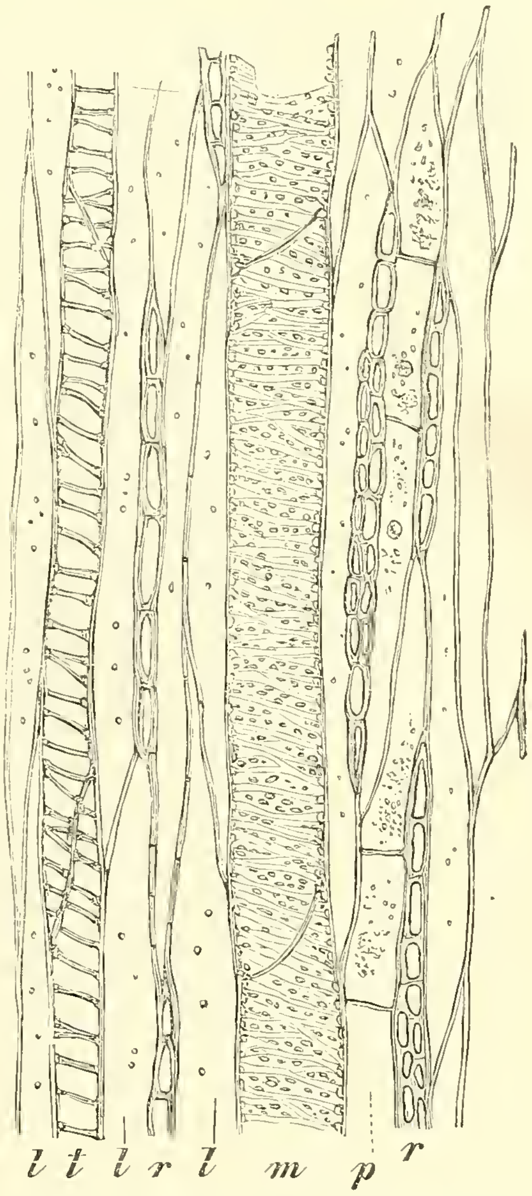


FIG. 149.—Tangential section of the wood of *Tilia parvifolia*. *m*, Pitted vessel; *t*, spiral tracheids; *p*, wood parenchyma; *l*, wood fibres; *r*, medullary rays. (× 160.)

The **Medullary Rays** of the Gymnosperms (Fig. 138, *ms*) and woody Dicotyledons (Fig. 146, *pm*, *sm*) form radial bands, composed wholly or in part of parenchymatous elements. Their function is to supply the cambium and wood with the products formed in the leaves and conveyed away by the bast. The medullary rays in this way link together by radial bands of living cells the protoplasm-containing elements of the bast and wood, thus uniting all the separate living tissues of the stem. The medullary rays are in turn accompanied or, if many-layered, traversed by intercellular air-cavities, which, beginning in the periphery of the stem, penetrate the cambium and communicate with all the intercellular spaces throughout the living elements of the wood and bast. All the living elements are kept in communication with the atmosphere by means of the intercellular spaces of the medullary rays, and the necessary interchange of gases is thus rendered possible.

The substances contained in the parts of the medullary rays within the wood, chiefly consisting of starch, tannins, resin, and crystals, are essentially the same as those in the wood parenchyma. In the medullary rays of certain Gymnosperms, particularly in the Pine, single rows of cells, without living contents and situated usually at the margin of the medullary bands, become tracheidal in structure (Figs. 142, 143, *tm*), and united with one another and with the tracheids by means of bordered pits. Their purpose is to facilitate the transfer of water radially between the tracheids. In other Conifers, where such tracheidal elements are not found in the medullary rays, bordered pits are developed in the tangential walls of the tracheids of the late wood, and by means of them is effected the transfer of water in a radial direction. The living cells of the medullary rays of the wood bear the same relation to the water-carriers as does the wood parenchyma, and like them are connected with the water-conducting elements by means of bordered pits. They take up water from them and give it out again, as it may be needed, to other living cells; on the other hand, in the spring, at the beginning of the season of growth, they press into the water-courses the products of assimilation, in particular glucose and small quantities of albuminates, in order that these substances may be transferred in the quickest way to the points of consumption. Accordingly, during the winter and in the beginning of spring, sugar and albumen may be detected in the tracheal elements ([72]), and may then be obtained from the watery sap of "bleeding" trees, or from artificial borings or incisions, particularly in such trees as the Maple, Birch, and Hornbeam. In the wood of Dicotyledons it is usually only special rows of the medullary ray cells which stand in such close relation with the tracheal tissues. In these special rows, generally on the margins of the medullary rays, the cells are elongated vertically, and on that account have been distinguished

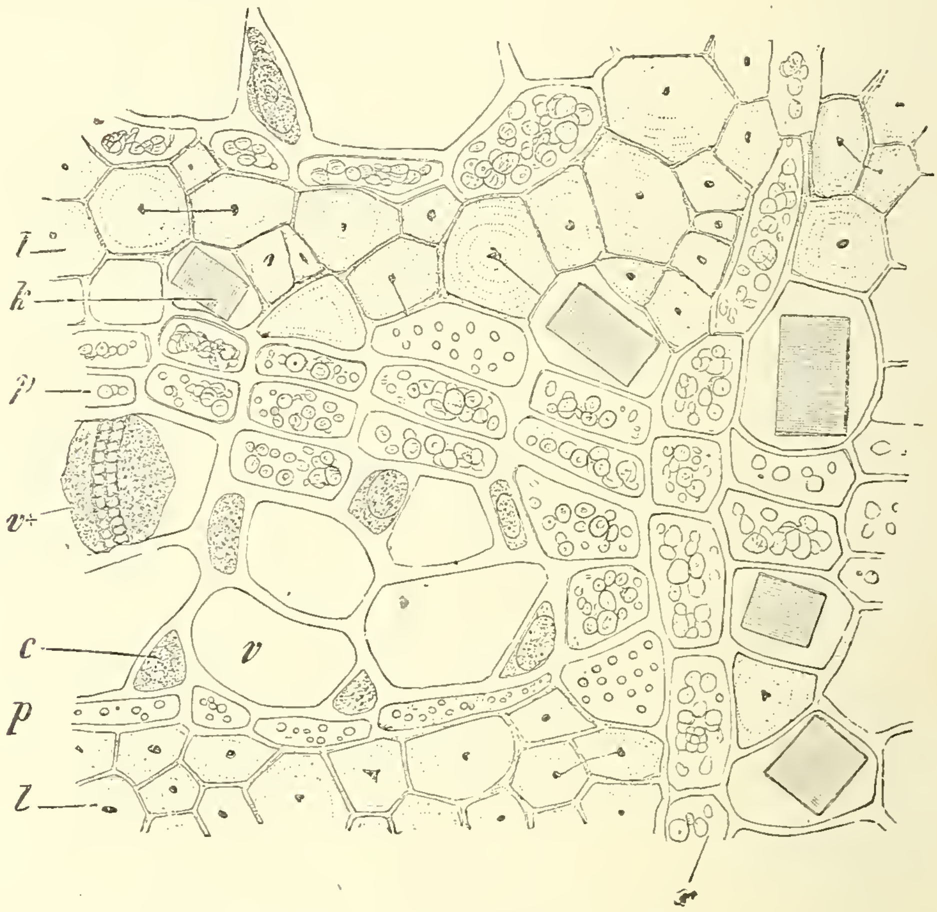


FIG. 150.—Portion of a transverse section of the bast of *Tilia parvifolia*. *v*, Sieve-tubes; *v**, sieve-plate; *c*, companion cells; *k*, cells of bast parenchyma containing crystals; *p*, bast parenchyma; *l*, bast fibres; *r*, medullary ray. (× 540.)

as VERTICAL MEDULLARY RAY CELLS. The other cells, or those of the middle layers of the medullary bands, on the other hand, are called HORIZONTAL MEDULLARY RAY CELLS; they are narrower and more elongated radially (73). These have, moreover, no especial connection with the tracheal elements, but are designed for conducting and storing assimilated matter. Within the bast zone the medullary rays are also distinguished as CORTICAL RAYS, and in the bast of Dicotyledons they have a simpler structure than in the wood. It is evident, not only from the connection existing between the cells of the medullary rays and the bast parenchyma, but also from the relations exhibited in Dicotyledons between the medullary ray cells and the companion cells of the sieve-tubes, that the function of the cortical rays is to take up the substances passing down the bast strands. For not only is the bast parenchyma in communication with the cells of the medullary rays by means of bordered pits, but the companion cells are so disposed on the sides of the sieve-tubes as more surely to come in contact with the medullary rays.

In the Pine and other *Abietineae*, whose bast parenchyma is devoid of cells functioning as conductors of albuminous matter, their place is taken in this respect by rows of medullary ray cells (Fig. 142, *em*). These maintain an intimate connection with the sieve-tubes by means of sieve-pits. They lose their contents in the same manner as the sieve-tubes, and, like them, become compressed and disorganised. On the other hand, the cells of the cortical rays, which contain starch, like the similar cells of the bast parenchyma, increase in size, and pushing between the compressed sieve-tubes, continue living for years.

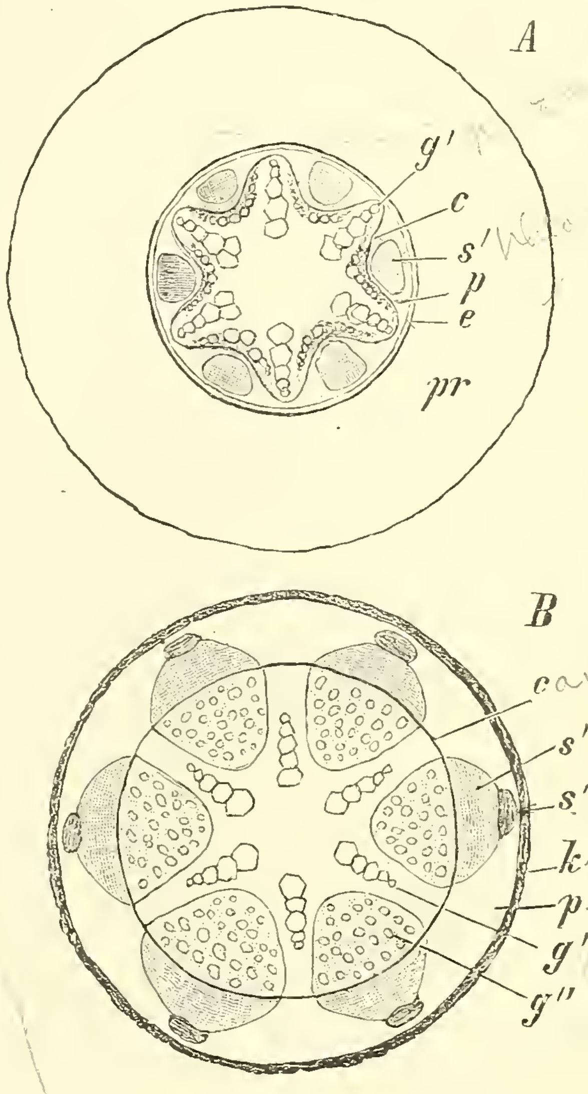


FIG. 151.—Diagrammatic representation of the growth in thickness of a dicotyledonous root. *pr*, Primary cortex; *c*, cambium ring; *g′*, primary vascular strand; *s′*, primary phloem strand; *p*, pericycle; *e*, endodermis; *g″*, secondary wood; *s″*, secondary bast; *k*, periderm.

The width and height of the medullary rays may be more easily determined from tangential than from radial sections. In such tangential sections the medullary rays appear spindle-shaped (Figs. 143, 149). With few exceptions, as in the Oak and Beech, the medullary rays are rarely of more than limited dimensions. The Oak, in addition to numerous small medullary rays, has other larger rays which may be as much as a millimetre broad and a decimetre high. In the Poplar, Willow, and Box the medullary rays are so extremely small that they are scarcely visible, even with the aid of a magnifying glass. The height of the broad primary rays of many Lianes, on the other hand, may be equal to that of a whole internode. In certain Conifers, resin-ducts occur not only in the wood, but also in the broader medullary rays. These radial resin-ducts are in communication with the vertical ducts. It is due to this fact that such a large amount of resin exudes from wounds in Pine or Fir trees.

Secondary Thickening of the Root in Gymnosperms and Dicotyledons.—The ROOTS of Gymnosperms and Dicotyledons, in which the stems increase in thickness, also show a similar GROWTH IN THICKNESS (74). Whenever secondary growth begins in a root with its xylem and phloem strands alternating with each other (Figs. 123, 128), areas of cambium arise on the inside of the phloem strands, through the division of the fundamental tissue; these give off wood elements towards the centre of the root, and bast towards the periphery. These cambium areas soon meet in the pericycle, just in front of the xylem strands, and so form a complete zone of meristematic tissue. In Fig. 151, *A*, this process is diagrammatically represented. As a result of the activity of its cells the cambium ring soon loses its sinuous form, and becomes a simple ring. In front of the primary vascular strands (*g'*), the cambium produces medullary ray tissue, and this constitutes the broadest medullary rays which lead to the strands of primary xylem (Fig. 151, *B*). A cross-section of such a root, in which the secondary growth has continued for some years, can scarcely be distinguished from a cross-section of a stem. By careful examination, however, the presence of primary tissue in the centre of the root can be discovered, and its nature thus determined. The wood of the root is also more porous than in the stem, and bears a close resemblance to spring-wood. On account of this lack of differentiation in the wood, the annual rings of growth are less distinctly defined in roots than in stems.

Anomalous forms of Growth in Thickness (75).—Extraordinary deviations from the usual type of secondary growth are afforded by some stems and roots of Gymnosperms and Dicotyledons. Among the Gymnosperms in the *Cycadaceae* and certain species of *Gnetum*, in the *Chenopodiaceae*, *Amarantaceae*, *Nyctaginaceae*, *Phytolaccaceae*, and other families of Dicotyledons, the cambium which has been formed in the ordinary manner soon loses its function, and a new cambium ring is developed external to the bast zone, for the most part in the pericycle, or in a tissue derived from it. This cambium ring forms wood on the inside and bast on the outside, with the accompanying medullary rays. It then ceases to divide, and a new ring takes its place. This process repeats itself, and ultimately leads to the formation of concentric wood and bast rings, which, in cross-sections of the sugar-beet, may be distinguished with the naked eye. These concentric zones may be still more plainly seen in a cross-section of *Mucuna altissima* (Fig. 152), a Liane belonging to the order *Papilionaceae*. The stem shows in this case an inner axis of wood (1) surrounded by a zone of bast (1*); next follows a cylinder of wood (2) and bast (2*), and finally a third (3, 3*) in process of formation in the midst of the pericycle. An extraordinary appearance is exhibited by cross-sections of stems, which show several separate wood cylinders (Fig. 153). Such a structure is peculiar to various tropical Lianes of the genera *Serjania* and *Paullinia* belonging to the family *Sapindaceae*. This anomalous condition arises from the unusual position of the primary vascular bundles, which are not arranged in a circle but form a deeply lobed ring; so that, by the development of interfascicular cambium, the cambium of each lobe is united into a separate cambium ring. Each of these rings, independently of the others, then gives rise to wood and bast (Fig. 153). An even more peculiar structure is exhibited by many Lianes of the *Bignoniaceae*, the wood of which is cleft by radially projecting masses of bast (Fig. 154). The primary stem of the *Bignoniaceae* shows the ordinary circular arrangement of the vascular bundles. Wood and bast are at first produced from the cambium ring in the usual manner, and form an inner, normal wood cylinder of AXIAL WOOD. Such normally formed axial wood cylinders are common to many, otherwise abnormally developed Lianes. The cambium ring of the *Bignoniaceae*, after performing for a time its normal functions, begins, at certain points, to give off internally only a

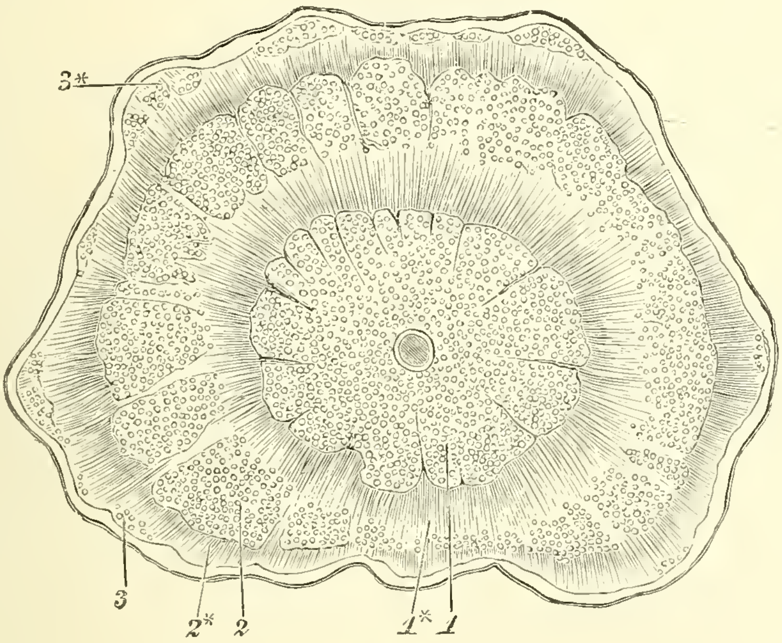


FIG. 152.—Transverse section of the stem of *Mucuna altissima*. 1, 2, 3, Successively formed zones of wood; 1*, 2*, 3*, successively formed zones of bast. ($\frac{3}{4}$ nat. size).

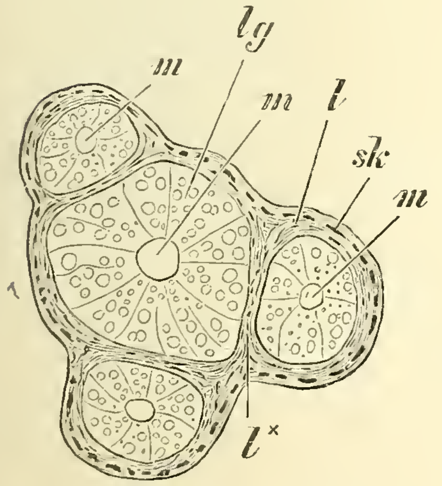


FIG. 153.—Transverse section of the stem of *Serjania Laruotteana*. *sk*, Part of the ruptured sclerenchymatous ring of the pericycle; *l* and l^*, bast zones; *lg*, wood; *m*, medulla. (× 2.)

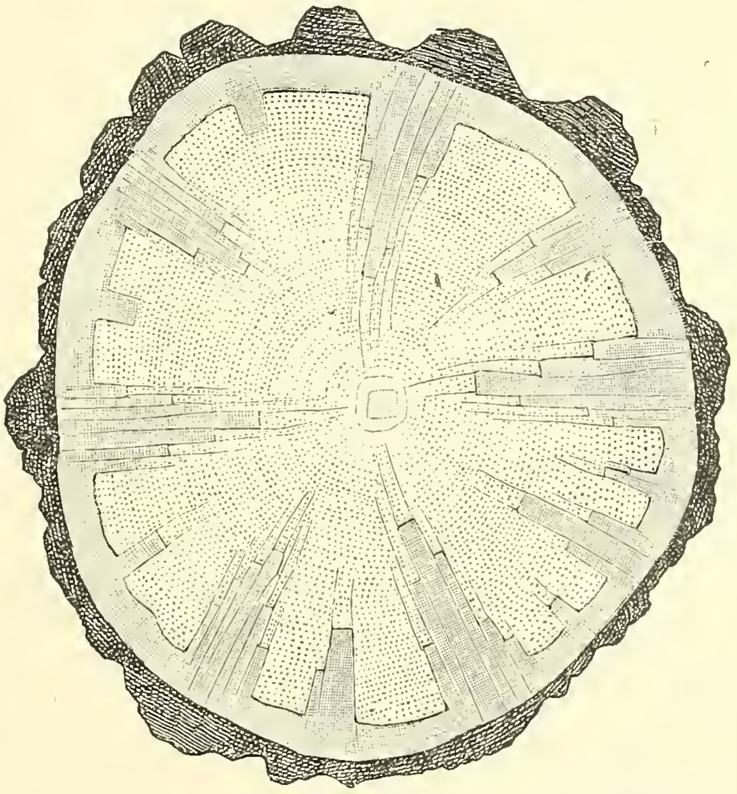


FIG. 154.—Transverse section of the stem of a *Bignonia*. (Nat. size.)

very small quantity of wood, and externally a correspondingly large amount of bast. As a result of this, deep wedges of irregularly widening bast project into the outer so-called PERIAXIAL WOOD (Fig. 154). The originally complete cambium becomes thereby broken into longitudinal bands, which are broader in front of the projecting wood than at the apices of the bast wedges. As the periaxial wood is always developed from the inside, and the wedges of bast from the outside of their respective cambium bands, they extend past each other without forming any lateral connection.

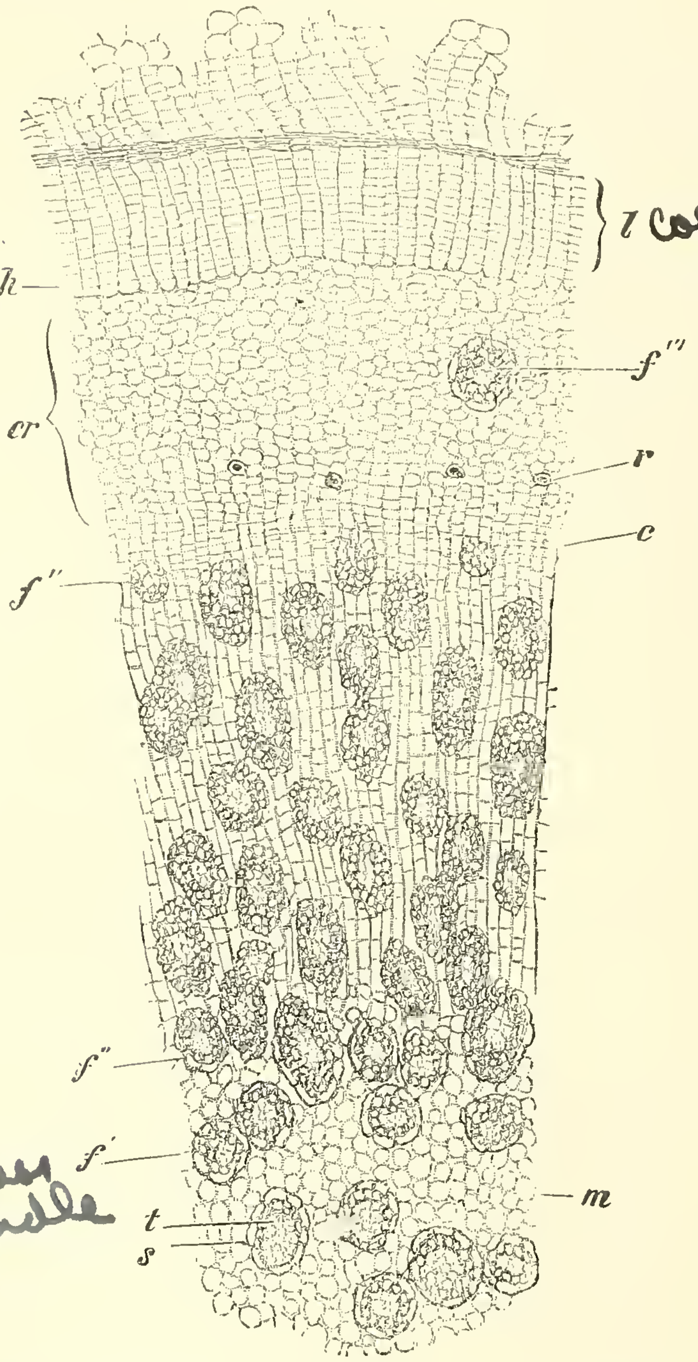


FIG. 155.—Transverse section of the stem of *Cordyline* (*Dracaena*) *rubra*. *f'*, Primary vascular bundles; *f''*, secondary vascular bundles; *f'''*, leaf-trace bundle within the primary cortex; *m*, parenchymatous fundamental tissue; *s*, bundle-sheath; *t*, tracheids; *c*, cambium ring; *cr*, cortex, the outer portion being primary, the inner secondary cortex; *ph*, cork cambium; *l*, cork; *r*, bundles of raphides. (× 30.)

Secondary Growth of Monocotyledons.—There are certain monocotyledonous plant families and genera, especially *Dracaena*, *Yucca*, *Aloe*, the *Dioscoreaceae*, and some Palms (76), in the stems and roots of which a cambium ring is developed. As in such cases, the cambium ring generally arises in the pericycle, outside the scattered vascular bundles and from the fundamental tissue, it is a secondary meristem; it does not, as in Dicotyledons and Gymnosperms, produce continuously wood and bast in opposite directions, but, instead, closed vascular bundle strands and fundamental tissue (Fig. 155).

Secondary Growth of Leaves (77) is always very slight, and is confined to a few *Coniferae* and Dicotyledons with evergreen leaves. The increase in thickness is due to the presence of a fascicular cambium. This produces little or no xylem, the new elements being mostly added to the phloem. Any elements formed on the side next the xylem are water-conducting, while those adjoining the phloem become sieve-tubes.

Periderm (78).—It is very seldom that the epidermis, by the division of its own cells, is in a condition to keep pace for any length of time with the increasing dimensions of the stem. This, however, is the case with the Mistletoe (*Viscum album*), the number of whose epidermal cells is continually augmented by the formation of new lateral walls, while the outer walls are at the same time strengthened by inward thickenings to supply the place of the older, ruptured, thickening layers. The stems also of one of the Maples (*Acer striatum*), even when a foot or more thick and over forty years old, remain covered with a living, growing, epidermal layer. As a rule, however, the epidermis on stems which grow in thickness becomes stretched and finally ruptured. The tissue of the primary cortex, by the expansion and division of its cells, can accommodate itself more easily than the epidermis to the increased dimensions of the stem, arising from the growth in thickness of the central cylinder. This process of cortical growth is particularly noticeable in the primary medullary rays (Fig. 146, *pm′*) between the primary phloem. The formation of the PERIDERM generally begins during the first vegetative period, after the secondary growth has reached a certain stage. The commencement of its formation is indicated by the brown colour of the external surface of the stem, which, however, remains green so long as the epidermis continues alive. The periderm is derived from a secondary meristem, termed the CORK CAMBIUM or PHELLOGEN. This phellogen may arise, in the epidermis, in a deeper layer of cells of the primary cortex, or even in the pericycle itself. The cells of the phellogen divide by tangential walls, and also, at times, by radial walls, in order to accommodate themselves to the increasing thickness of the stems. Of the new cells thus formed, those given off towards the periphery of the stem are the CORK CELLS (Fig. 155, *l*). They usually have a tabular shape, fit closely together without intercellular spaces, and possess suberised, secondary, thickening layers. The cork cells are, for the most part, filled with air, containing also a yellow or brown substance, and usually possess brown walls. The cell walls may be thin or thick, frequently thickened on one side, and occasionally to such an extent that they are known as stone cork. The cork tissue frequently shows an alternation of thick-walled and narrow with thin-walled and larger cells. These layers mark annual growths. The cork cells, being impermeable to water, prevent the loss of moisture by transpiration, while at the same time they shield and protect the inner tissues.

The cork of the Cork-oak (*Quercus Suber*) is formed of broad layers of soft large cells, alternating with narrow and thinner layers of cells, which mark the limit of the annual growth. This may be seen in bottle-corks. The first, spontaneously developed cork of the Cork-oak is stripped off, whereupon a new phellogen is formed in the deeper-lying tissue. The cork thus produced is removed every six or eight years, and furnishes the cork of economic value.

In many cases the phellogen takes its origin in the epidermis (Fig. 156). This is the case in the Willow, in all *Pomaceae*, and in a great number of other woody plants. The epidermal cells become divided into outer and inner cells, the latter of which assume the function of a phellogen. More frequently the phellogen develops from the layer of cells next adjoining the epidermis, as, for example, in the Elder (*Sambucus nigra*), where it takes its origin from the outermost layer of collenchyma (Fig. 157, *ph*).

At the same time that the cork is forming from the outer side of the phellogen, a so-called CORK CORTEX or PHELLODERM is also frequently developed from its inner side. The cells of the phelloderm retain their living protoplasm, and usually contain chloroplasts. They ultimately become rounded off, so that intercellular spaces are formed between them. The term periderm includes both cork and phelloderm.

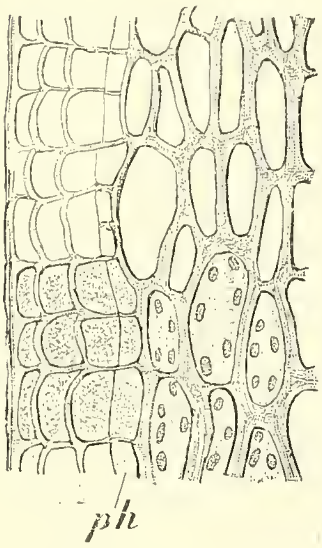


FIG. 156.—Transverse section of the peripheral tissues of a one-year-old twig of *Pirus communis* at the beginning of the formation of periderm. *ph*, Phellogen. (× 300.)

Bark.—All tissues external to the phellogen are cut off from food supplies, and consequently die. When the first cork layer has its origin deep within the stem, a BARK is formed through the ensuing death of the excluded peripheral tissues. If the cork layer formed by the phellogen be thin, the stem has a smooth surface, as in the Beech; if it produces thicker cork layers, the surface of the stem appears rough and full of fissures, as is the case in the Cork-oak. The primary phellogen generally ceases its activity after a short time, and another deeper-lying phellogen is formed. After a time this new phellogen discontinues its functions, and another (Fig. 158) is developed, as in the case of *Quercus sessiliflora*, until ultimately the phellogen comes to be formed in secondary bast parenchyma instead of in the primary tissue. That portion of the bast cut off by the periderm loses its nutritive contents and only retains waste products. If the layers of the secondary periderm constitute only arcs of the stem circumference, the bark will be thrown off in scales, as in the SCALY BARK of the Pine and Plane tree; if, on the contrary, the periderm layers form complete concentric rings, then hollow cylinders of the cortical tissues are transformed into the so-called RINGED BARK, such as is found in the Grape-vine, Clematis, and Honeysuckle. Bark which is not easily detached becomes cracked by the continued growth in thickness of the stem, and has then the furrowed appearance so characteristic of the majority of old tree-trunks. The usual brown or red colour of bark, just as in similarly coloured heart-wood, is occasioned by the presence of tannins, to the preservative qualities of which is due the great resistance of bark to the action of destructive agencies. The peculiar white colour of Birch-bark is caused by the presence of betulin (birch-resin) in the cells.

In roots which grow in thickness the phellogen usually develops in the pericycle (Fig. 151, *B*, *k*), and in consequence of this the primary cortex of the roots dies and peels off. The succeeding phellogen layers are formed in exactly the same way in the root as in the stem.

Lenticels (79).—In most woody plants, particularly in Dicotyledons, cortical pores, or LENTICELS (Fig. 157), make their appearance simultaneously with the formation of periderm. The lenticels take their origin in a phellogen layer (*pl*) which, in the case of peripheral cork formation, almost always develops directly under the stomata. The phellogen, from which the lenticels arise, unlike the cork phellogen, does not form cork cells, but a lenticel tissue composed of COMPLEMENTARY CELLS (*l*) traversed by intercellular spaces. On the inside, however, a phelloderm is regularly derived from the phellogen. The complementary cells press the epidermis outwards and finally rupture it. Where the complementary cells are only loosely united, intermediate bands or closing layers are developed from the phellogen alternately with the layers of looser tissue; the closing layers become eventually ruptured. The cork-forming phellogen joins the phellogen of the lenticels at its margins. In cases where the cork is more deeply seated in the inner tissue, the lenticels begin their development at a corresponding depth. Lenticels serve to maintain the gaseous interchange between the outside air and the gases present in the intercellular spaces of the plant.

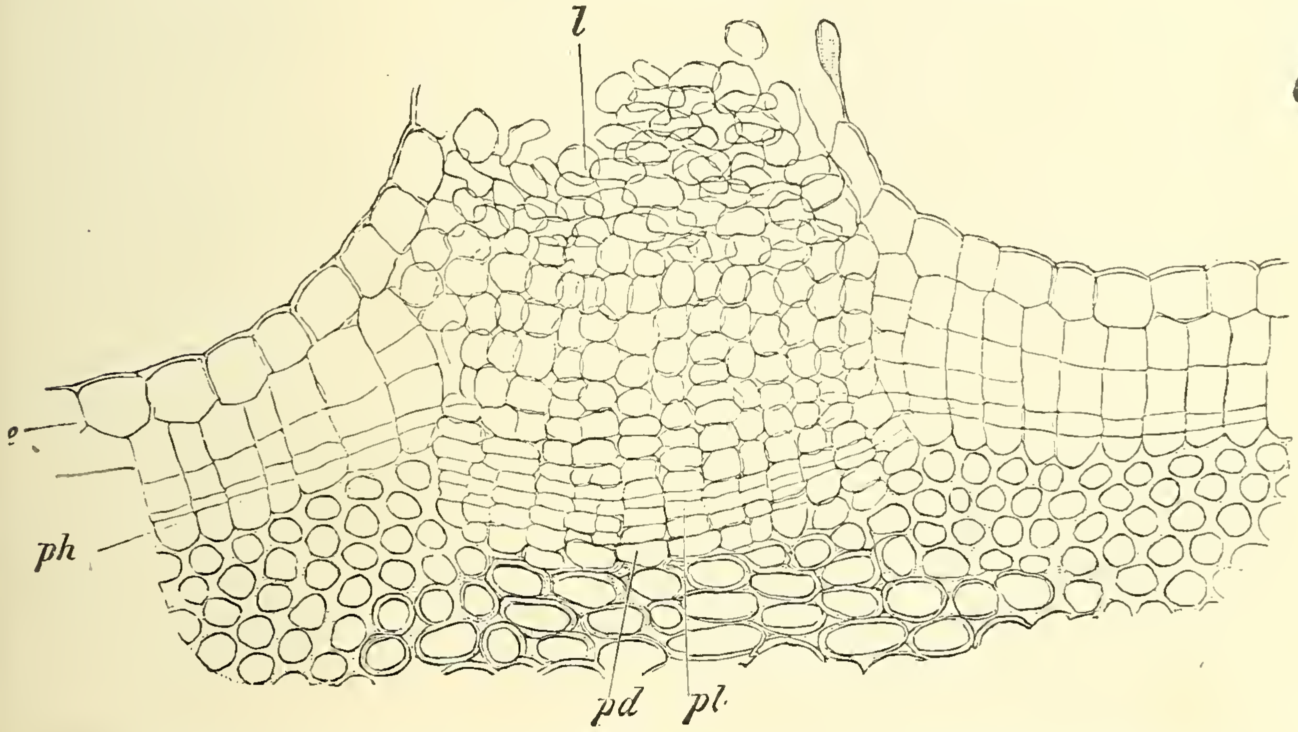


FIG. 157.—Transverse section of a lenticel of *Sambucus nigra*. *e*, Epidermis; *ph*, phellogen; *l*, complementary cells; *pl*, phellogen of the lenticel; *pd*, phelloderm. (× 90.)

The Falling of Leaves (80).—Preparatory to the falling of leaves an absciss layer is formed, by means of which the separation of the leaves from the stem is effected. This layer arises through the division of all the living cells in the plane of separation, including even those of the vascular bundles. At a later stage, a layer of cells in the middle of the absciss layer becomes absorbed, and the separation of the tissues of leaf and stem is completed by the rupture of the tracheal elements and sieve-tubes. The absciss layer is usually formed just before the leaves fall, although frequently much earlier. The wound left on the stem either simply dries up, as is the case in the Ferns, or it is closed by a layer of cork, which is formed just below the surface and joins the periderm of the stem. This cork layer may be formed before the fall of the leaves, but in that case it does not extend through the living elements of the vascular bundle, and does not become complete until after the leaves have fallen. The ends of the tracheal elements at the leaf-scars become filled with a protecting gum, and in addition, they, as well as the ends of the sieve-tubes, become compressed and finally cut off by the developing cork.

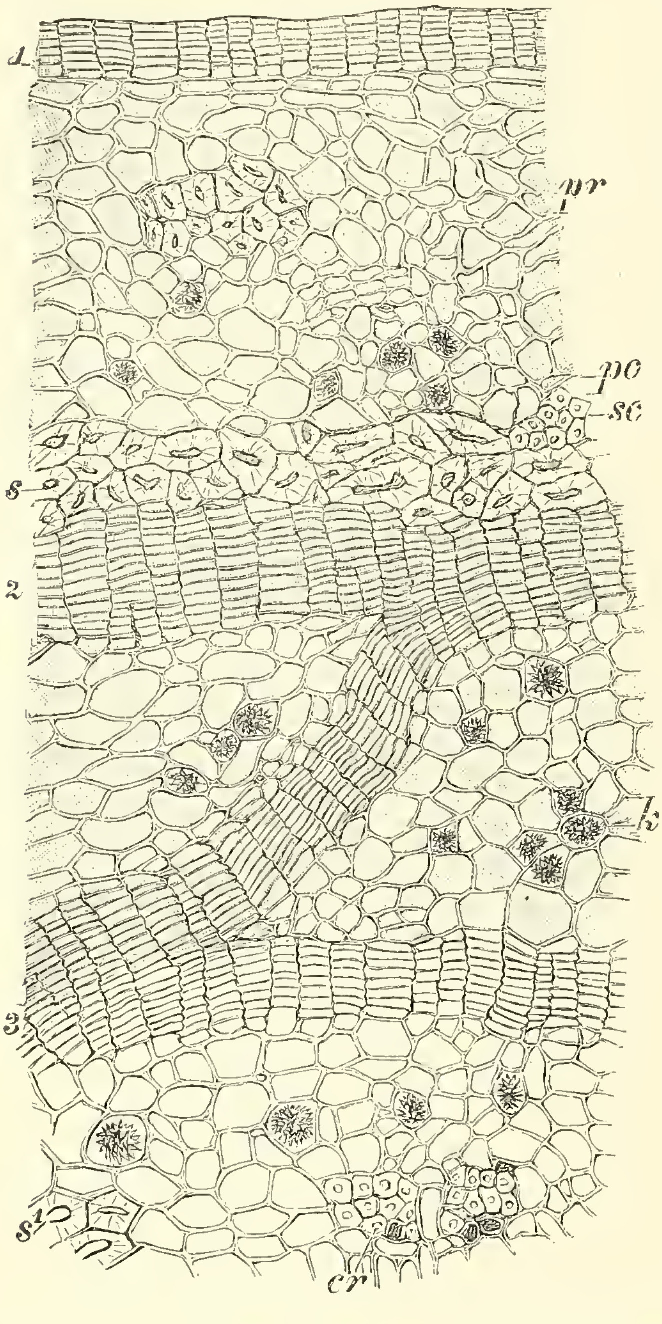


FIG. 158.—Transverse section of the peripheral tissues of the stem of *Quercus sessiliflora*. 1, 2, 3, Successively formed layers of cork; *pr*, primary cortex, modified by subsequent growth; internally to *pc*, pericycle; *sc*, sclerenchymatous fibres, from the ruptured ring of sclerenchymatous fibres of the pericycle; *s*, subsequently formed sclereids; *s'*, sclereids, of secondary growth; *cr*, bast fibres with accompanying crystal cells; *k*, cells, with aggregate crystals. All of the tissue external to the innermost layer of cork is dead and discoloured, and has become transformed into bark. (× 225.)

Wounds.—In the simplest cases the exposed tissues of wounded surfaces become dry through loss of moisture, and dying in consequence, form over the deeper-lying tissues a protective covering of dry, brown cells. This method of protecting wounded surfaces, although very general in Cryptogams, rarely obtains in Phanerogams, but instead the wounds become closed by the formation of cork. Cork formed over wounded surfaces is called WOUND CORK. It is derived from a cork cambium that develops in the tissue under the wounds, and with its development the process of healing, in succulent and parenchymatous portions of plants, is completed. In woody plants a so-called CALLUS is formed by the active growth of the living cells bordering on the wound. These abnormal swollen growths close together over the wound, and by the suberisation of their cell walls provide a sufficient protection. Generally, however, a cork-forming phellogen arises in the periphery of the callus. In stems of Gymnosperms and Dicotyledons, wounds which extend into the wood become surrounded and finally overcapped by an outgrowth of tissue arising from the exposed cambium. While the callus tissue is still in process of gradually overgrowing the wounded surface, an outer protective covering of cork is developed; at the same time a new cambium is formed within the callus, through a differentiation of an inner layer of cells, continuous with the cambium of the stem. When the margins of the overgrowing callus tissue ultimately meet and close together over the wound, the edges of its cambium unite and form a complete cambial layer, continuing the cambium of the stem over the surface of the wound. The wood formed by this new cambium never coalesces with the old wood. Accordingly, marks cut deep enough to penetrate the wood are merely covered over by the new wood, and may afterwards be found within the stem. In like manner, the ends of severed branches may in time become so completely overgrown as to be concealed from view. As the wood produced over wounds differs in structure from normal wood, it has been distinguished as CALLUS WOOD. It consists at first of almost isodiametrical cells, which are, however, eventually followed by more elongated cell forms.

The Formation of Burrs.—The curled or extraordinarily knotted appearance of wood, such as the bird's-eye or curled maple, which adds so much to its technical value, is due to the unusually sinuous course taken by the elements of the wood. This variation from their usual direction is caused by the development of numerous adventitious buds, which turn the vascular bundles out of their accustomed course; the direction of the wood elements is moreover often affected by the medullary rays, which sometimes become so abnormally swollen that they appear almost circular in tangential sections.

The Phylogeny of the Internal Structure

The phylogenetic differentiation in the internal structure of a plant does not altogether coincide with the progress of its external segmentation. Even unicellular plants in the group of Siphoneous Algæ may exhibit a high degree of external differentiation; thus the unicellular Alga, *Caulerpa* (Fig. 253), has developed appendages having outwardly the form of leaf, stem, and root. Similarly, the red seaweed, *Hydrolapathum* (Fig. 9), although composed almost wholly of one form of cells, bears in its external segmentation a striking resemblance to one of the most highly organised plants. The internal differentiation of this Alga has only advanced so far, that the outer cells containing the red chloroplasts form an assimilating tissue of isodiametrical cells, while the internal colourless and more elongated cells function as a conducting tissue. The relatively highest degree of internal development found in the Algæ is attained by the *Laminariae.* In their stem-like axis, which may have a considerable thickness, the external tissues frequently contain canals filled with mucilaginous matter; while internally are found rows of cells resembling sieve-tubes (60). The axes themselves grow in thickness through the continuous division of the cells of an outer cell layer. A kind of cortical tissue is formed as a result of this growth which exhibits concentric layers, and of which the innermost cells gradually elongate and pass over into the so-called medulla. In the Fungi internal differentiation is the result of the more or less intimate union of the intertwining hyphæ. In extreme cases the hyphæ forming the body of the Fungus may be so closely woven together as to give, in a cross-section, the impression of a parenchymatous tissue (Figs. 105, 106), in which, by the subsequent thickening of the cell walls, the pits in adjoining hyphæ are brought into contact. In the fructifications of many of the *Hymenomycetes* and *Gasteromycetes*, some of the longer and more swollen hyphæ contain a cloudy, highly refractive, and, in some instances, coloured substance, and appear, accordingly, to serve as a special tissue for the purpose of conduction. A marked advance in the differentiation into different tissue systems is first apparent in the Bryophytes, and even in them the formation of an epidermis distinct from the fundamental tissue is exceptional. In the thallus of the *Marchantieae* of the *Hepaticae*, and at the base of the spore capsules of the *Bryineae*, among the Mosses, the external layer of cells becomes more or less sharply defined from the underlying tissues. In the *Marchantieae* (Fig. 159) this outer layer is pierced by openings which have been termed breathing-pores, but these have a different origin from the stomata of higher plants. They are rather, as LEITGEB (81) has shown, openings into cavities, which have

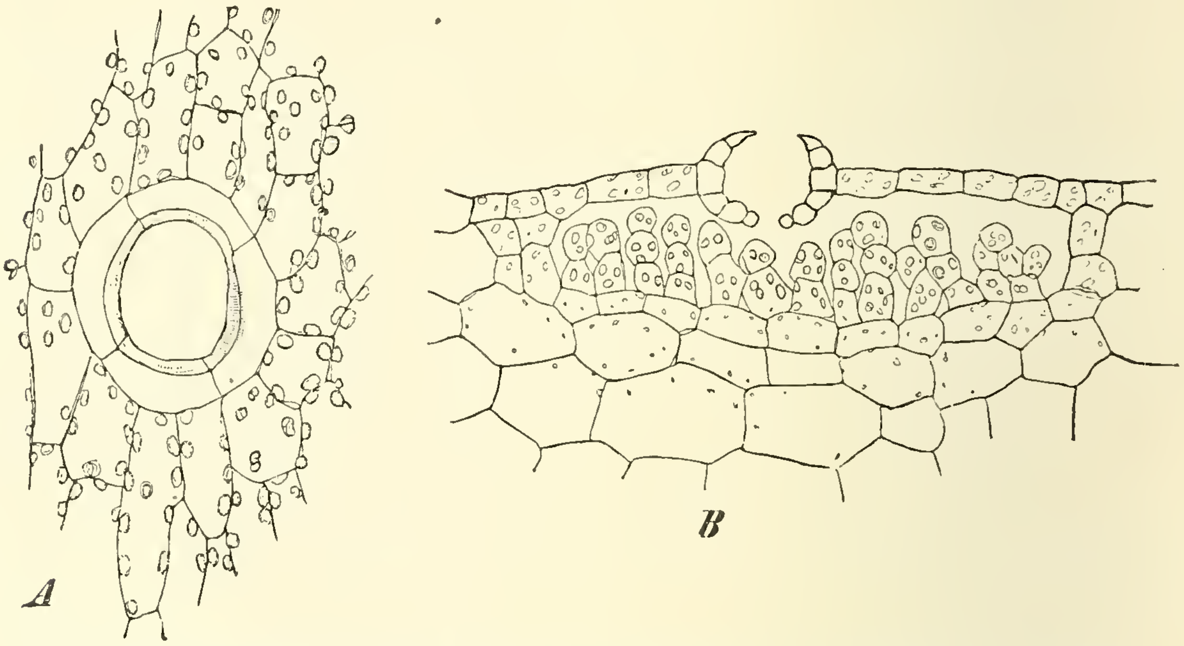


FIG. 159.—Surface and transverse view of the thallus of *Marchantia polymorpha.* In *A*, an air-pore, as seen from above; in *B*, as seen in cross-section. (× 240.)

arisen through the overarching of certain portions of the surface by other more rapidly growing portions. In the *Bryineae*, on the other hand, stomata similar in structure to those of the Pteridophytes and Phanerogams are found in the outer cell layer at the base of the spore capsules. It would seem, however, that these stomata of the *Bryineae* are probably not homologous with those of higher plants, as there is no direct phylogenetic connection between them, and it is more reasonable to regard them as merely analogous formations, such as so often occur in the evolution of organs. In the stems of many of the *Bryineae* there is also developed a simple form of conducting tissue (Fig. 160); and the many-layered midrib of the single-layered leaf lamina is also traversed by a conducting strand. In spite of their more advanced differentiation, the Bryophytes may still be included, just as they were originally in 1813 by DE CANDOLLE ([82]), in his classification of the vegetable kingdom according to the natural system, with the other lower Cryptogams in the class of CELLULAR PLANTS, as distinguished from the VASCULAR PLANTS or Pteridophytes and Phanerogams. A separation of the tissues into the three systems of tegumentary, fundamental, and vascular tissue occurs for the first time in the vascular plants associated with the development of roots; while the systems themselves also exhibit a widely extended differentiation.

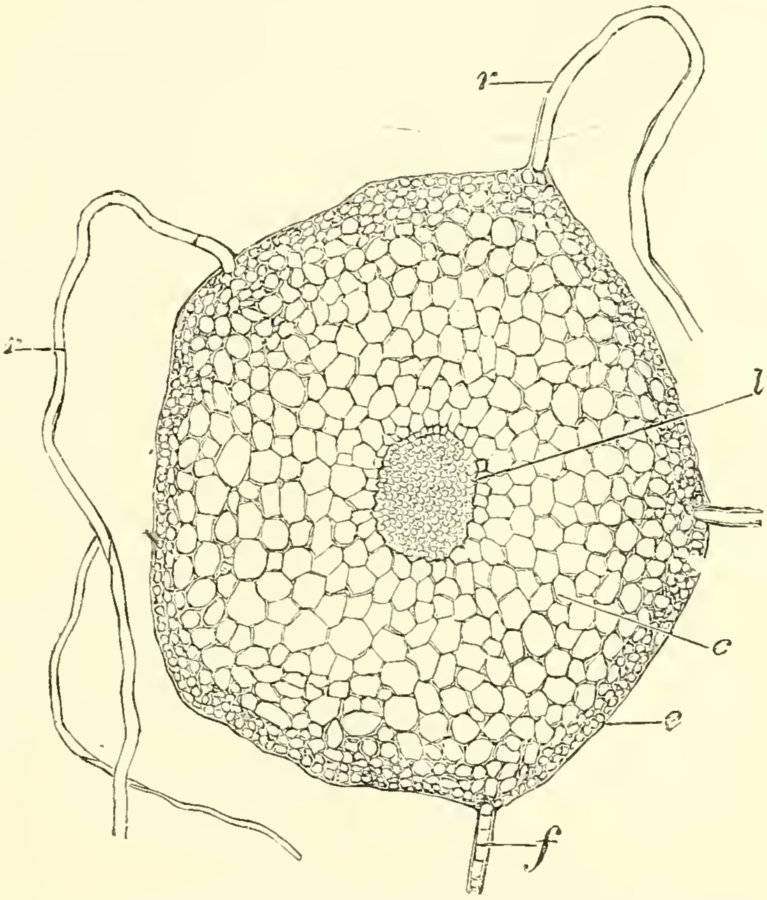


FIG. 160.—Transverse section of the stem of *Mnium undulatum*. *l*, Conducting-bundle; *c*, cortex; *e*, peripheral cell layer of cortex; *f*, part of leaf; *r*, rhizoids. (× 90.)

The Ontogeny of the Internal Structure

However a plant may arise, whether from an asexually produced spore or from a fertilised egg, its first inception is always as a single cell. In unicellular, spherical, or rod-shaped organisms, such as *Gloeocapsa polydermatica* (Fig. 1) or Bacteria (Fig. 4), the whole course of development is concluded with the cell division which gives birth to two new independent organisms. If the cell divisions be continuous and parallel, and the newly-developed cells remain in contact, CELL FILAMENTS (Fig. 4, *a**) will be formed; if the division walls have different inclinations, and are at the same time all in the same plane, CELL SURFACES are produced; and if the walls are formed in three dimensions of space, CELL MASSES are the result. Such an organism will attain but a low degree of development if all its cells have a like value, and continuously reproduce themselves in the same manner. With the distinction into BASE and APEX a plant manifests a higher degree of differentiation. A VEGETATIVE or GROWING POINT is then developed, usually at the apex, and in the simpler cases this consists of but a single cell (Fig. 5). The apex assumes more and more the character of an APICAL CELL from which all the organs of the plant take their origin; thus, in the case of *Cladostephus verticillatus* (Fig. 7), the many-celled main axis terminates in a single conical cell which, by transverse and longitudinal divisions, gives rise to the cellular system of the whole plant. Its side branches are likewise formed from similar apical cells, which develop, in regular acropetal order, from certain of the lateral cells of the parent stem, and determine the character of the branching, to which reference is made in the specific name of this sea-weed. Flat, ribbon-like plants also, such as *Dictyota dichotoma* (83) (Fig. 8), may have conical but correspondingly compressed apical cells (Fig. 161, *A*), from which segments are cut off by concave cross walls, and become further divided by subsequent longitudinal walls. The dichotomous branching so apparent in *Dictyota* is preceded by a longitudinal division of the apical cell into two equal adjoining cells (*B*, *a*, *a*). By the enlargement and continuous division of these two new apical cells the now bifurcated stem becomes prolonged into two forked branches. In other ribbon-like *Algæ*, on the other hand, and in similarly shaped *Hepaticae*, as in *Metzgeria* and *Aneura* (84), the apical cell is wedge-shaped (Fig. 162), and the

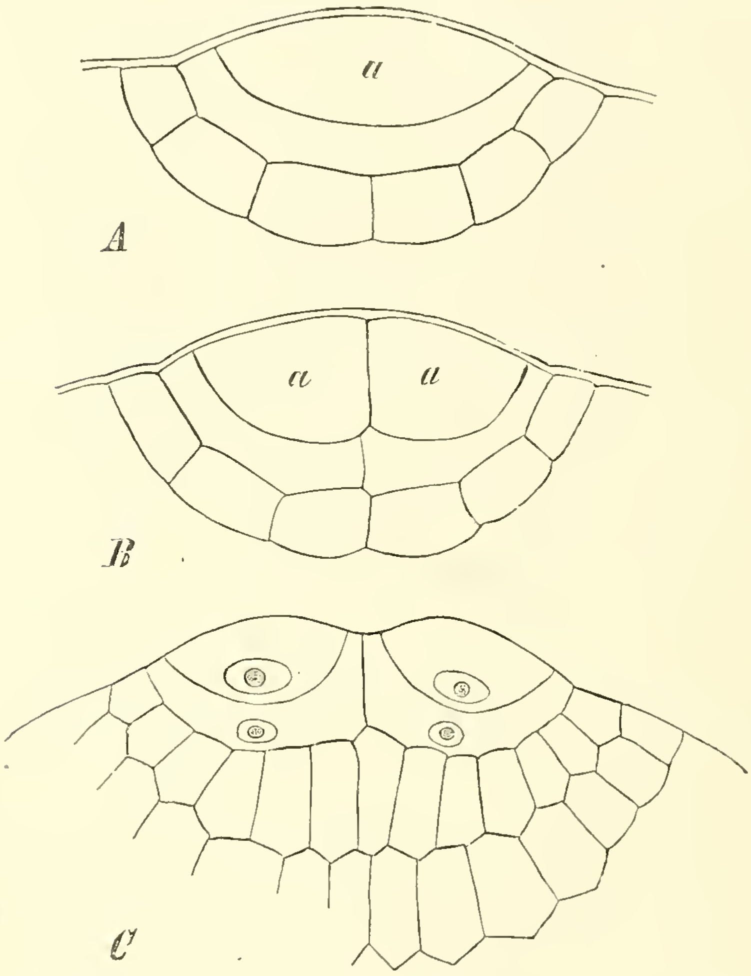


FIG. 161.—The growing point of *Dictyota dichotoma*, showing the dichotomous branching. *A*, Initial cell. (After E. DE WILDEMAN, × 500.)

successive segments are cut off alternately right and left by intersecting oblique walls; from these segments the whole body of the plant is derived by further division. The apparently strictly dichotomous branching of *Hepaticae* provided with such apical cells is in reality due to the early development of new apical cells in young segments (Fig. 162, *b*). In the case of the erect radially symmetrical stems of the *Musci*, most Ferns and *Equisetaceae*, the apical cell has generally the shape of an inverted pyramid ([85]) with a convex base, and forms the apex of the vegetative cone characteristic of the more highly organised plants. In the Common Horsetail (*Equisetum arvense*), for example, the apical cell of the main axis viewed from above (Fig. 164, *A*), appears as an equilateral triangle, in which new walls are successively formed in a spiral direction, parallel to the original walls (*p*). Each new segment thus derived is divided by a new division wall (Figs. 163, 164, *m*) into an upper and lower half; each of these halves, as is shown most clearly by an optical section just below the

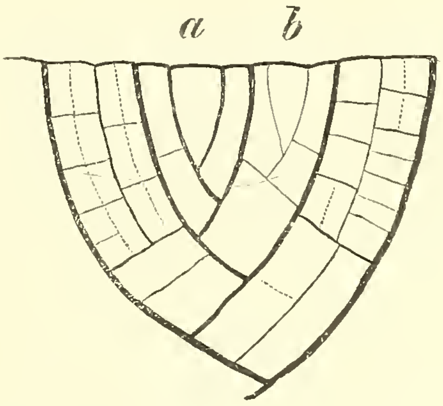


FIG. 162.—Diagrammatic representation of the apex of *Metzgeria furcata* in process of branching, viewed from the dorsal side. *a*, Apical cell of parent shoot; *b*, apical cell of daughter shoot. (After KNY, × circa 370.)

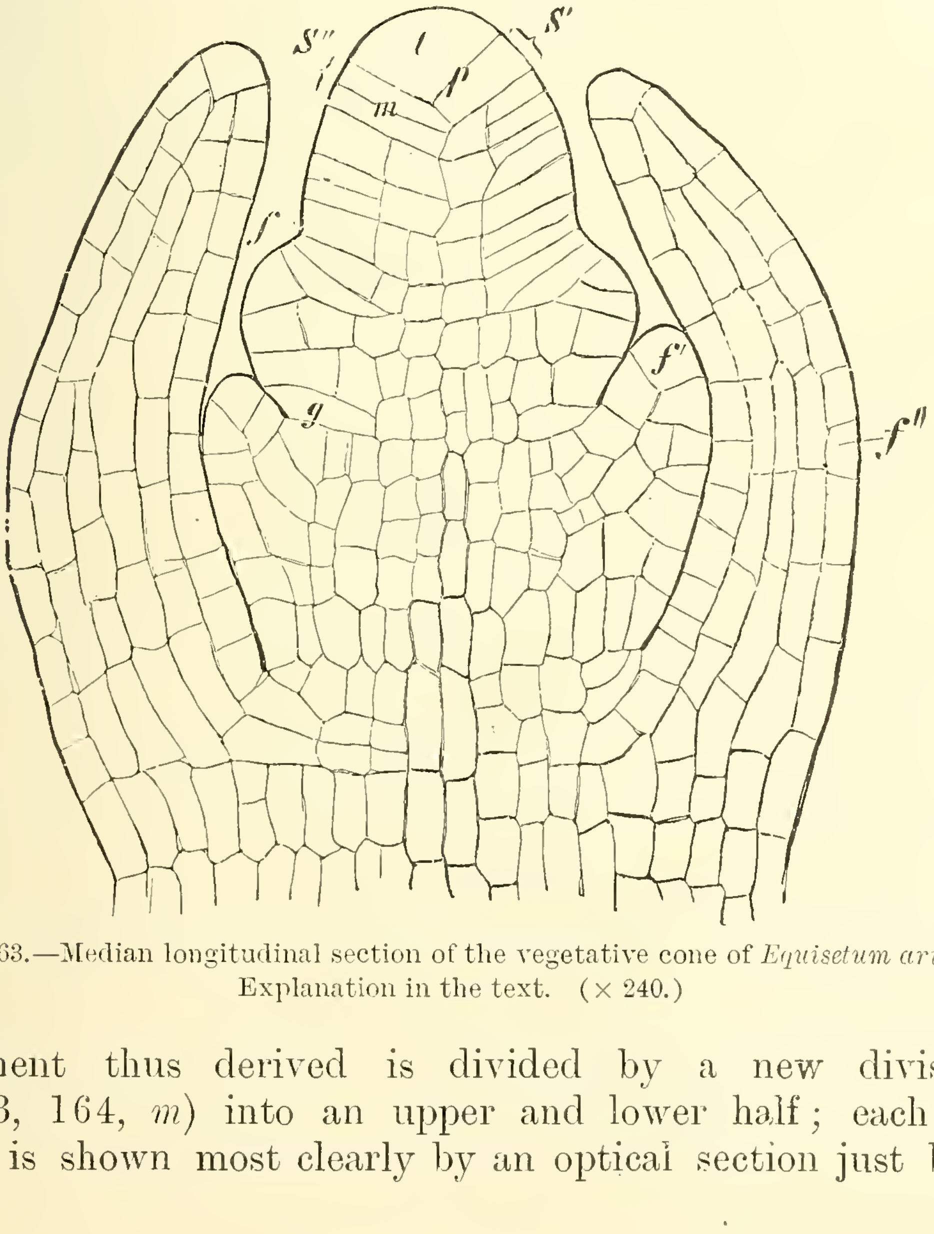


FIG. 163.—Median longitudinal section of the vegetative cone of *Equisetum arvense*. Explanation in the text. (× 240.)

apical cell (Fig. 164, *B*), becomes again divided by a sextant wall (*s*) into two new cells. It is unnecessary to trace the further divisions, and it will suffice to call attention to the fact, that all cell walls parallel to the outer surface of such vegetative cones or portions of plants are termed PERICLINAL WALLS, while such as meet the surface and the periclinal walls at right angles are designated ANTICLINAL, of which those in the plane of the axis of an organ are called RADIAL. Some distance below the apical cell of *Equisetum arvense* the first leaf-whorl arises from the vegetative cone as a circular wall, which grows by the formation of cell walls inclined alternately inwards and outwards in the wedge-shaped marginal cells which form its surface layer (Fig. 163, *f*). This is succeeded at a lower level by other and older leaf-whorls (*f′*, *f″*). An initial cell (*g*) may be distinguished in the axil of the second leaf-whorl, and this is destined to become the three-sided apical cell of a side branch.

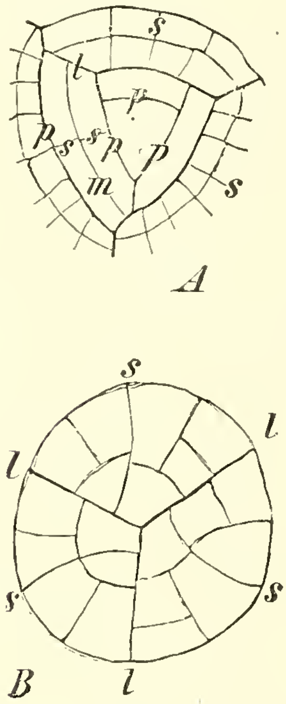


FIG. 164.—*A*, Apical view of the vegetative cone of *Equisetum arvense*; *B*, optical section of the same, just below the apical cell; *l*, lateral walls of the segments. (× 240.)

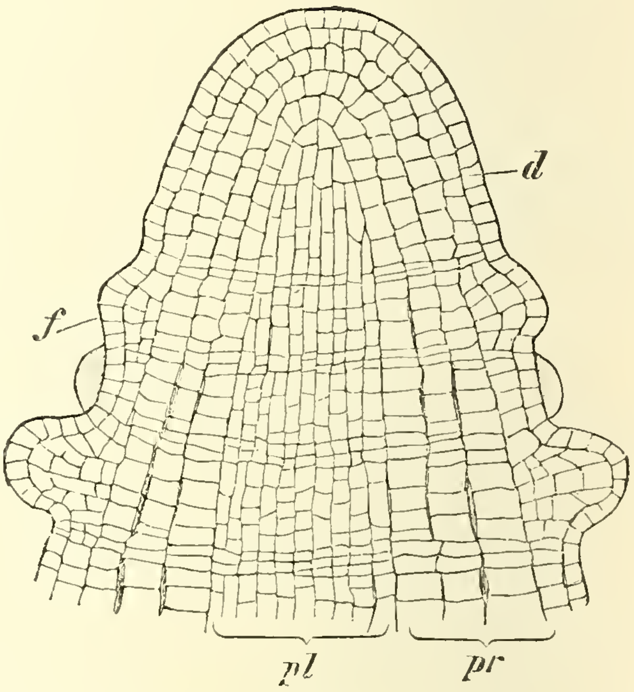


FIG. 165.—Median longitudinal section of the vegetative cone of *Hippuris vulgaris*. *d*, Dermatogen; *pr*, periblem; *pl*, plerome; *f*, leaf rudiment. (× 240.)

In the *Lycopodinae*, the most highly developed of the Pteridophytes, a distinct apical cell can no longer be recognised, while in the Phanerogams the cells of the vegetative cone are arranged as shown in the accompanying figure of *Hippuris vulgaris* (Fig. 165), in which the embryonic tissues are arranged in layers which, as was first noticed by SACHS (86), form confocal parabolas. The outermost layer, which covers both the vegetative cone and also the developing leaves, is distinguished as the DERMATOGEN (87) (*d*); the cells of the innermost cone of tissue, in which the central cylinder terminates, constitute the PLEROME (*pl*); while the layers of cells lying between the dermatogen and plerome are called the PERIBLEM (*pr*). In the same figure may be noticed the uniformity with which the dividing walls of the different layers intersect at right angles. This arrangement was regarded by SACHS as characteristic of the whole plant structure. The anticlinal walls at right angles to the surface form a system of orthogonal trajectories for the periclinal walls.

While SACHS regarded the insertion of new cell walls at right angles to preexisting ones as the principle of their succession, BERTHOLD and ERRARA (88) have endeavoured to show that the curvature and mode of insertion of a partition wall obey the same laws as do weightless films of liquid. The cell wall tends at the moment of its origin to assume the same position as a film in a mass of soap-suds would under similar conditions.

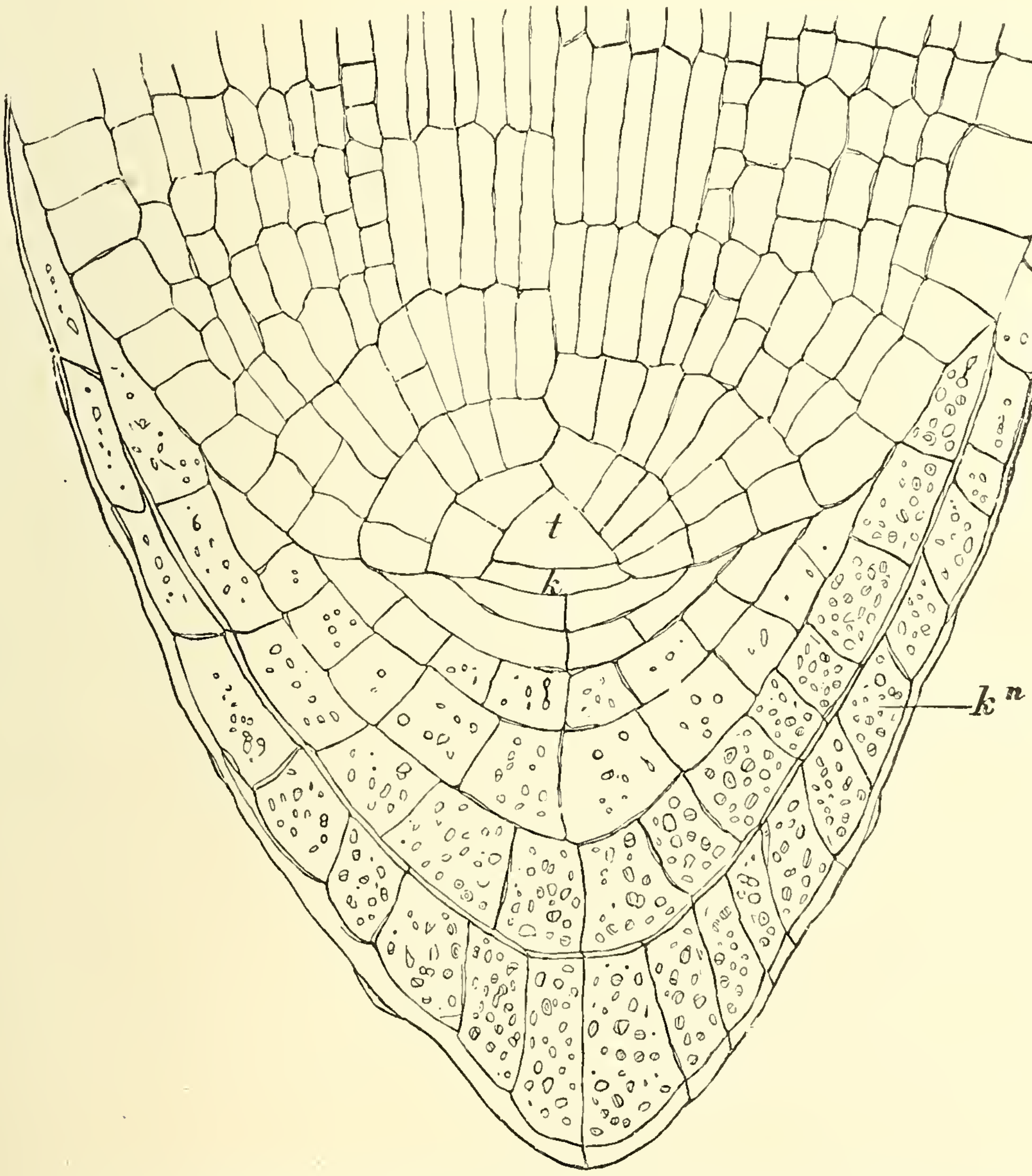


FIG. 166.—Median longitudinal section of the apex of a root of *Pteris cretica*. *t*, Apical cell; *k*, initial cell of root-cap; k^n, root-cap. (× 240.)

True ROOTS are first found in the Pteridophytes, and possess an apical cell in the shape of a three-sided pyramid (89) (Fig. 166, *t*). In addition to the segments given off by the apical cell parallel to its sides, it also gives rise to other segments (*k*) parallel to its base. It is from the further division of these latter cap-like segments that the ROOT-CAP is derived. In the roots, as in the stems of the *Lycopodinae*, no apical cells are found. In like manner the roots of Phanerogams, although exhibiting several different types of root-growth, follow the same law in the arrangement of their elements as the vegetative cone of the stems. It will, accordingly, be sufficient to describe a root of one of the *Gramineae* (Fig. 167) as a representative of one of these types (^{90}). The vegetative cone of this root differs from that of the stem previously described (Fig. 165) in the possession of a root-cap.

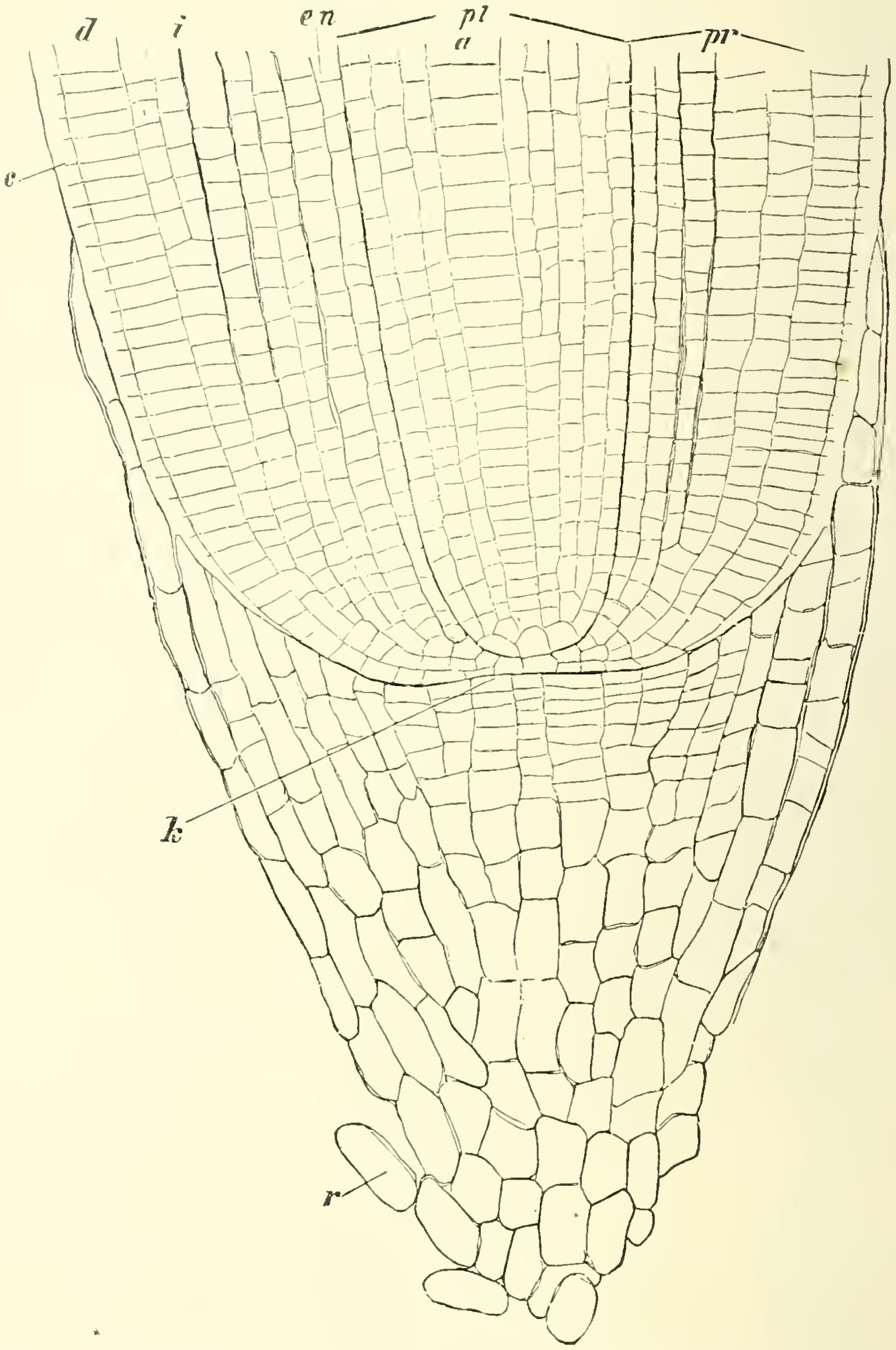


FIG. 167.—Median longitudinal section of the apex of a root of the Barley, *Hordeum vulgare*. *k*, Calyptrogen ; *d*, dermatogen ; *c*, its thickened wall ; *pr*, periblem ; *pl*, plerome ; *en*, endodermis ; *i*, intercellular air-space in process of formation ; *a*, cell row destined to form a vessel ; *r*, exfoliated cells of the root-cap. (× 180.)

The dermatogen (*d*) and periblem (*pr*) unite at the apex in a single cell layer, outside of which lies the CALYPTROGEN (*k*) or layer of cells from which the root-cap takes its origin. In many other roots, however, the formation of the root-cap results from the periclinal division of the dermatogen itself, which, in that case, remains distinct from the periblem. In the apices of Gymnosperms the dermatogen, periblem, and calyptrogen are not marked out as distinct regions. In roots, as in stems, the plerome cylinder (*pl*) almost always terminates in special initial cells.

At a short distance below the growing point the embryonic tissue loses its meristematic character, and becomes transformed into the differentiated body of the plant. As a general rule, in plants with an epidermis, primary cortex, and central cylinder, the epidermis is developed from the dermatogen; the primary cortex from the periblem; the central cylinder from the plerome. This differentiation of the tissues does not take place in all cases; and, in fact, does not extend to the embryonic tissue, the peculiar cell arrangement of which is due rather to physical causes. The vascular bundles must pass through the periblem in order to reach the leaves. The periblem is therefore capable of producing, not only the primary cortex, but also the vascular bundles and accompanying tissues of the central cylinder. The terms dermatogen, periblem, and plerome are employed merely for convenience to designate certain cell layers, and are not to be regarded as significant of any peculiar histogenetic or tissue-forming ability. The external layer from which the epidermis develops usually remains a single cell layer. The rudiments of the still undeveloped vascular bundles soon appear in the central cylinder as procambium strands; while the endodermis of roots is derived at an early stage from the innermost layer of the cortex.

In stems with apical cells THE RUDIMENTS OF NEW LEAVES and SHOOTS are developed from single peripheral cells, or cell groups of the vegetative cone (Fig. 163). In such cases, not only the new shoots, but even the leaves, usually begin their development with an apical cell. The apical cells of the leaves, however, soon disappear, and further growth proceeds along their whole margin.

In a stem with no apical cell (Figs. 17, 165) the rudiments of the leaves and new shoots first appear as small protuberances, the formation of which is generally initiated by the periclinal division of a group of periblem cells; while, in the meantime, the cells of the overlying dermatogen continue their characteristic anticlinal divisions. In the case of new shoots developing at some distance from the growing point of the parent stem, the cells from which they are destined to arise retain for that purpose their original embryonic character. In spring the formation of the buds on the rapidly growing shoots of bushes and trees may be postponed, so that the rudimentary lateral shoots first appear in the axils of the eighth or even the tenth youngest leaves, and consequently at points where the differentiation of the surrounding tissue has already begun (^{91}).

The vegetative cone, in the case of strictly dichotomously-branching shoots (cf. p. 19), increases the number of its cells in the direction of the plane of the subsequent bifurcation, and eventually gives rise to two new growing points.

With the exception of those *Pteridophytes*, whose roots as well as stems are dichotomously branched, the branches of the roots arise in acropetal succession; and their branching first begins in regions considerably removed from the growing point, and where the differentiation of the tissues is already complete. In Phanerogams new roots are developed in the pericycle: in Pteridophytes in the innermost cortical layer. The lateral roots must consequently push through the whole cortical layer of the parent root. They are situated either directly in front of the vascular strands of the parent root, or between the xylem and phloem strands. The number of rows of lateral roots is, therefore, as VAN TIEGHEM (^{92}) has pointed out, either equal to or double the number of vascular strands. As the strands of the vascular bundles of roots take a straight course, the lateral roots must similarly form straight rows. The distances between the rows themselves are equal, or when the lateral roots are situated to the right and left of each vascular strand, the rows are arranged in pairs with wider intervals between each pair.

Inasmuch as a multicellular plant begins its development as a single cell, either from a spore or fertilised egg, and then gradually passes into its multicellular condition with corresponding internal and external differentiation, IT REPEATS IN ITS ONTOGENY THE STEPS OF ITS PHYLOGENETIC DEVELOPMENT. These phylogenetic processes, however, undergo material modification in the course of the ontogenetic development of a plant. The internal modifications are in some respects less marked than those experienced by the external organs, because the internal inherited structure is less subject to the disturbing action of external influences. The ontogeny of the internal differentiation of a plant is on this account often of service in determining its relationships. In most cases, it may be safely said that every change in the internal differentiation of an organ is of more general significance the earlier it manifests itself in the development of the embryo, and the nearer it occurs to the growing point in which the embryonic development is continued. Conversely, a characteristic is so much the more significant for the determination of immediate relationships, the later it makes its appearance in the ontogenetic development.

Structural Deviations (^{93})

Plants, even of the same species, never exactly resemble each other. Every individual organism has its own peculiar characteristics by which it may easily be distinguished from every other of the same species. To a certain extent individual variability may be due to ATAVISM, or the reappearance of previous ancestral qualities. Most individual deviations belong, however, to the so-called FLUCTUATING VARIATIONS. These occur in all species, and may be compared to the excursions of a pendulum to either side of its position of equilibrium. Besides these fluctuating variations, a progressive change of the species is also met with, which finds its expression in a common deviation of the individuals. This has been termed MUTATION by HUGO DE VRIES (94). Individuals which have deviated in this way are as a rule characterised by the change affecting their whole organisation, and not single organs only. The changes tend, moreover, to be strongly inherited. Abrupt and striking deviations of the individual from the type of the species are called MONSTROSITIES. When these induce a disturbance of function a diseased condition results. The causes of variations, mutations, and monstrosities lie in the organism itself, and for the most part remain obscure. In other cases they are determined by external influences, and then may sometimes be subjected to experimental treatment. As an example of VARIATIONS OCCASIONED BY INTERNAL CAUSES may be cited the so-called BUD-VARIATIONS, which result in the abnormal development of single shoots. In like manner a variation in the number of the members of a floral or leaf whorl may occur as a result of internal causes; thus, for example, *Paris quadrifolia* occasionally exhibits a hexamerous instead of a tetramerous symmetry. The internal structure of a plant may likewise be disturbed, and the development of its vascular water-courses or of its mechanical elements become considerably altered. In many cases variations are, no doubt, the result of changes in the mode of nutrition; this fact has been taken advantage of by horticulturists to bring about certain wished-for results. Among EXTERNAL CAUSES OF VARIATIONS the influence exercised by parasites upon the development of the whole plant is particularly striking. *Euphorbia Cyparissias*, when attacked by a rust fungus (*Aecidium Euphorbiae*), becomes sterile, remains unbranched, has shorter and broader leaves, and in its whole appearance is so changed as scarcely to be recognisable. Plant lice sometimes cause a flower to turn green, so that instead of floral leaves green foliage-like leaves appear. Another peculiar example of abnormal growths are the GALLS or CECIDIA produced on plants by Fungi, or more frequently by insects. The effect of these formations on the normal development of the tissues of a plant is more or less disturbing, according to their position, whether it be in the embryonic substance of the growing point, or in the tissues still in course of differentiation, or finally in those already developed. The larvæ of *Cecidomyia rosaria* live in the growing points of willow stems, and occasion a malformation of the whole stem by the production of galls known as "willow-roses." Flies (*Diptera*) often deposit their eggs in the tissues of partially developed leaves, in consequence of which the leaves become more or less swollen and twisted. After the leaves of the Oak have attained their full growth they are often stung by a gall-wasp of the genus *Cynips*. The poison introduced by the sting, and also by the larvæ hatched from the eggs deposited at the same time, occasion at first only a local swelling of the leaf tissue, which finally, however, results in the formation of round, yellow, or red galls on the lateral ribs on the under side of the leaf. As galls materially differ from one another according to the nature and cause of their formation, it is generally possible to determine the insect or Fungus by which they were induced. As an explanation of malformations which originate in the plants themselves, some exciting cause must be presumed which turns the processes of development from their usual course. The earlier such an influence makes itself felt in the rudiments of organs the more severe is its effect upon their development. When the embryonic substance of the growing point is affected by such an influence, altogether unexpected modifications of the usual order of growth may result. As the embryonic substance of the growing point is of itself capable of producing all such forms as are peculiar to the species, instead of a flower a vegetative shoot may be developed, or the growing point of a root may continue its further development as a stem. Leaves, even when somewhat advanced in growth, may under changed conditions vary their usual character, particularly within the limits of their possible metamorphosis; for example, the staminal and carpellary leaves of a flower may thus become transformed into additional perianth leaves. The later the rudiments of an organ are acted upon by a disturbing influence, so much the less far-reaching are the modifications which it produces; and thus intermediate forms between two organs may be produced which correspond more or less closely to one or the other of them. Finally, through the capability of a fully-differentiated tissue to renew, as a secondary meristem, its embryonic condition, an organ of an entirely different morphological value may be produced instead of one already in process of formation; in this way, for example, a shoot may take the place of a spore capsule. Consequently neither the abnormal interchangeability, at times manifested between morphologically different members, nor the development of intermediate forms between them, can be considered as proof of their phylogenetic connection. MALFORMATIONS ARE, ACCORDINGLY, NOT TO BE ACCEPTED AS EVIDENCE IN MORPHOLOGICAL QUESTIONS, EXCEPT IN THE RARE CASES WHEN THEY MAY BE CONSIDERED AS A REAPPEARANCE OF ANCESTRAL QUALITIES.

PART I

GENERAL BOTANY

SECTION II

PHYSIOLOGY

SECTION II

PHYSIOLOGY

PLANTS, like animals, are living organisms. Beginning their development with the simplest structure, and increasing in size from internal causes, they assume their definite form and complete their existence according to laws determined by inheritance. Surrounded by a world, which differs very widely from them as regards chemical constitution, they produce the substances necessary to their growth from the raw materials afforded by the environment. To this end the different parts of their bodies are enabled by independent movements to take such relative positions as are most favourable to their mode of growth. In spite of the number of individuals and the limited duration of life, the continuance and extension of the species are provided for by an ability to reproduce like organisms.

NOURISHMENT, INDEPENDENT GROWTH, POWER OF MOVEMENT, and REPRODUCTION are, together with RESPIRATION, the striking attributes which characterise plants as living organisms, and distinguish them from all lifeless bodies.

An organism consisting of but one cell, as is shown by the life of the simplest plants, is capable of exercising all the functions necessary for the continuance of its existence. In the case of plants, however, which consist of many hundreds or thousands of cells arranged in three dimensions of space, it is impossible, for purely physical reasons, that all the cells should bear the same relations to the outer world. The cells in the interior must exist under conditions altogether different from those which are in direct contact and intercourse with the world outside. Consequently, the differently arranged elements must be adapted for different modes of life, and, since they must exercise their functions in different ways, must show what is called DIFFERENTIATION.

This necessary division of labour has led to the development of external organs and internal structures wonderfully adapted to the requirements of the whole plant. Correlated with the various Classes and relationship of plants, there are certain differences as regards form and function. But, in all plants, those organs to which the same functions are assigned have assumed the form most efficient for their purpose; so that, for example, the leaves and roots of plants otherwise most dissimilar are constructed on the same general plan. In proof of this may be cited the general terms leaf, root, stem, and flower, the comprehensiveness of which is even more evident in popular speech than in the technical language of Botany, which has given to these terms a more strictly defined and limited meaning.

Similarity in the appearance and structure of organs indicates the exercise of common functions and duties; while dissimilarities in the form and structure of different organs—such as the leaf and root—are indicative, on the other hand, of their different utility to the plant. There lies, then, in the morphological and anatomical development of an organ an unmistakable proof that it exists because of its function, and that it is not of accidental origin.

The attributes and functions of organs, as well as of single cells, are the subjects of physiological study. It is evident, however, that such study must be based upon an intimate knowledge of the outer and inner structure of plants; just as the working and efficiency of a machine first become comprehensible through a knowledge of its construction. On the other hand, the study of external and internal Morphology becomes animated by Physiology, and attains thereby a deeper purpose and meaning.

It is the province of Physiology to discover the points of correspondence among the numerous individual phenomena, and to bring to light such as possess an essential functional significance. On the other hand, it is the variations, or family peculiarities, which are of value in Systematic Botany, since from them a knowledge of family relationships may be derived. For example, it suffices for the physiological conception of flowers to know that they are the organs of sexual reproduction in higher plants; that the male cells are somehow developed from the pollen formed in the anthers; that from the female cells enclosed within the ovules, after their union with male cells, the embryos or rudimentary plants are derived. These important facts are equally true for all flowers, no matter how dissimilar they may appear.

Physiology considers peculiarities of form in so far as they are of service for special purposes arising from the relation of the plant to its surroundings (Pollination, Distribution of Seeds, Water-plants, etc.). This side of physiology is termed BIOLOGY, or better ŒCOLOGY, since the former term is often applied to the science of living beings in general.

The Physical and Vital Attributes of Plants

With the exception of the more or less fluid developmental stages in some of the lower organisms, as in *Amœba* or the plasmodia of

Myxomycetes, plants, in spite of the great amount of water contained in them, are of the nature of solid bodies. As such they possess in common with inanimate objects the physical attributes of weight, density, elasticity, conductivity for light, heat, electricity, sound, etc. Important as these attributes are for the very existence and continuance of the life of a plant, they do not constitute that life itself.

VITAL PHENOMENA ARE ESSENTIALLY BOUND UP WITH THE LIVING PROTOPLASM. No other substance exhibits a similar series of remarkable and varied phenomena, such as we may compare with the attributes of life. As both physics and chemistry have been restricted to the investigation of lifeless bodies, any attempt to explain vital phenomena solely by chemical and physical laws could only be induced by a false conception of their real significance, and must lead to fruitless results. The physical attributes of air, water, and of the glasses and metals made use of in physical apparatus, can never explain qualities like nutrition, respiration, growth, irritability and reproduction. It would, indeed, be superfluous to emphasise the fact, were it not that this error is from time to time repeated.

The phenomena of life can only be studied and determined by the most careful observation and critical examination of living organisms. It is therefore necessary to establish what part the purely physical and chemical properties, which belong to all bodies, take in the phenomena of life, and to what extent they are essential to the maintenance of life itself. A perception of the strictly physical and chemical processes going on within an organism is especially desirable, because operations are then involved with the causes and effects of which we are already familiar. In questions regarding strictly vital phenomena the case is quite different; for it then becomes impossible to predict what effect a particular cause will produce.

The free end of a horizontally extended flexible rod bends downwards merely by its own weight. The same result will follow if any part of a dead plant, such as a dry stem, be substituted for the rod. But if a living, growing stem be used in the experiment, then the action of gravity will manifest itself in a manner altogether at variance with its ordinary operation. That part of the stem which is still in a state of growth will ultimately curve upwards, and BY ITS OWN ACTIVITY ASSUME AN UPRIGHT POSITION; it moves in a direction exactly contrary to the attractive force of gravity. If a tap-root be similarly experimented upon, it will, on the contrary, continue its downward movement until it places itself in a line with the direction of the attraction; a rhizome, however, under like circumstances, would constantly maintain its growing apex in a horizontal position. In these three experiments the force of gravity is exerted upon flexible portions of plants. The physical conditions are the same in each case, yet how entirely different the results!

The explanation of this dissimilarity in the effects of the action of gravity is to be sought in the fact that gravity acts upon living substances, not only physically but also in another way, as a stimulus which induces a response in the internal forces of the plant body. In these particular experiments it is the force of growth which, locally, either increases or restricts the force of gravity, and produces results which do not correspond either qualitatively or quantitatively with the known operations of the laws of gravity. Living substance is dominated by the operation of stimuli. Irritability is its most important attribute, for it is irritability alone that renders possible what we call life.

By irritability is meant the undoubted, though not fully understood, connection between external stimuli and the response of a living organism. The disproportion that may exist between a cause and its ultimate effect is plainly apparent in a steam engine in motion or in the firing of firearms. The slight pressure of the finger in firing a cannon has as little correspondence, either quantitatively or qualitatively, with the destructive effect of the shot, as the small effort necessary to open the throttle-valve of a locomotive to the continuous motion of a heavily-laden goods train. The opening of the valve of an engine before the steam is up has no effect; it is only when, by this process, the compressed steam is liberated that it is followed by such enormous results. In the engine the connection between the cause and its effect is known; in the effects of stimuli on protoplasm this connection is not apparent, for in the protoplasm the intermediate processes remain invisible to the eye, even when aided by the best microscope. There is, however, no occasion for the supposition that the connection between the stimulating cause and its effect on the protoplasm is accomplished by processes which are otherwise foreign to the protoplasm itself, and which are called into existence only under the influence of a special force, the vital force. It was formerly thought necessary to ascribe not only all indications of life, but even all the transforming processes carried on within animate objects, to the effects of a special vital force or principle. Now, however, the conception of the vital processes has become so modified as no longer to require the supposition of such a special vital force; while the impossibility of explaining the manifold variety of their manifestation by the action of a single force, and the advances made in chemistry (cf. p. 5), have shown the futility of such a supposition.

Although, at the present time, the existence of a special, independent vital force is denied by Physiology, and only such agencies are accepted as are inherent in the substance of an organism itself, still we must at the same time take account of such a vital force in so far as it may be regarded as the expression of a living substance, endowed with a peculiar, internal structure, which is in some way so constituted that certain actions and conditions are followed by definite vital processes. It is, then, this peculiar quality of irritability that distinguishes living protoplasm from other bodies, and which constitutes the fundamental distinction between living and dead protoplasm. Such a view is, however, not contrary to accepted ideas; simple chemical bodies, indeed even chemical elements, such as sulphur, phosphorus, etc., exist in different "modifications" with fundamentally different peculiarities. In considering living organisms, it is the irritability or living modification of the protoplasmic substance which must occupy the attention. The object, therefore, of Physiology consists principally in discovering the attributes and characteristics incident to the modifications of living protoplasm.

These attributes and characteristics are so distinctive as to separate by a wide gap living bodies from all other matter. It is, in fact, impossible to form any conception of the manner in which living bodies have arisen on this once molten planet from lifeless matter. Acceptance of the theory of evolution authorises, it is true, the transfer of the inception of life on the earth to geological periods separated by millions of years from the present time; but the initiative character of such dawning life remains no less incomprehensible. From a consideration, however, of the attributes of the living substance, it can with safety be said that the external conditions of life could not at that time have been so very different from those now existing on the earth; for it is a characteristic quality of living matter that its vital activity, even its very existence, is circumscribed and limited by external, cosmic influences. The vitality of vegetable protoplasm can only be preserved within a definite range of temperature, while its full vital activity is restricted to still narrower limits. Too intense light or too little warmth destroys its life; while the most minute quantities of certain poisons suffice to shatter instantly and irrevocably that mysterious structure, in which, under favourable conditions, lies concealed the capacity to vivify the whole world.

Although living plants are themselves responsible for the manner in which their vital phenomena manifest themselves, they stand, nevertheless, in the closest reciprocal relations with their environment, upon the condition of which they are altogether dependent. From the outer world they obtain not only their nourishment, but receive also from it, particularly from the vibrations of light and heat, the energy that they again expend in the manifold processes of their vital phenomena. It is to the operation of these external influences that the stimuli are due, which constantly call forth in vegetable protoplasm the manifestation of vital phenomena. These external influences, however, are only serviceable to the processes of life when they operate within definite limits of intensity. The lowest limits of intensity for the effective operation of an external influence is designated the MINIMUM, the highest the MAXIMUM, while that degree of intensity at which it is most operative in calling forth the most active manifestation of a definite vital phenomenon is termed the OPTIMUM. For the different vital processes of the same plant, and also for those of distinct plants, these so-called CARDINAL POINTS are generally different.

The cardinal points for the vegetation of cold climates are on the average much lower than those of plants inhabiting temperate or tropical countries. The distribution of plants over the surface of the earth is thus to a considerable extent dependent on their cardinal points. The highest are not, however, possessed by tropical plants, but by small Algæ and Bacteria which inhabit hot springs, the water of which has a temperature of 70°-80° C. The albumen of a hen's egg is quickly coagulated by the water in which these plants find their suitable habitat. Some thermogenic Bacteria can raise their own temperature to 70° C., and even higher.

Some plants flourish best when exposed to bright sunlight, while the shade-loving plants only attain their perfect development in a subdued light, such as that of a forest. Not only does the intensity of the required illumination differ for different species of plants, and also for individuals of the same species, but it may be inconstant even for the same plant. Shade is absolutely essential for many tropical plants in a young state, although at a later age they can endure and may even require the full light of the tropical sun.

On exposure to a low temperature, about the freezing point of water, most plants become frozen and generally die. Very sensitive plants may even become frozen at a temperature considerably above zero, before ice has been formed in their tissues. In the case of other plants the internal formation of ice in their tissues does not of itself occasion death. The formation of ice always begins in the intercellular spaces and not within the cells. Its continued formation is accompanied by an increasing concentration of the cell sap; as a consequence of this, ice first begins to form in plants at a temperature below zero, and only gradually increases in case of a greater reduction of temperature. Such plants as inhabit Arctic and Alpine regions are able to recover from the completely frozen condition. The power which the lower organisms have of withstanding extremely low temperatures is very striking. In PICTET's investigations *Diatomaceae* were found to sustain a long exposure to a temperature of – 200° C.; MACFADYEN and others have shown that many Bacteria can endure a week's exposure to 250° of cold produced by means of liquid air and hydrogen (1).

A sudden change of temperature leading to the complete thawing of frozen plants is more favourable than repeated transitions from freezing to thaw. A long, keen frost is therefore, as a rule, less injurious to vegetation than a less severe frost alternating with frequent partial thaws.

I. The Stability of the Plant Body

One of the most important and essential physical attributes of a plant is its rigidity. Without that quality plants could retain no enduring form. The capacity to return, by their own independent movement, to favourable positions from which they may have been forcibly disturbed by external influences, is, in trees and shrubs, and also in the more rigid herbs, restricted to the extreme tips of the growing stems.

How great are the demands made upon the stability of plants will be at once apparent from a consideration of a rye haulm; for although it is composed of hundreds of thousands of small chambers or cells, and has a height of 1500 mm., it is at its base scarcely 3 mm. in diameter. The thin stems of reeds reach a height of 3000 mm. with a base of only 15 mm. diameter. The height of the reed exceeds by two hundred times, and that of the rye haulm by five hundred times, the diameter of the base. In comparison with these proportions our highest and most slender buildings, such as tall chimneys, are extremely thick structures; in them the height is only from twelve to seventeen times the diameter of the base. In addition, moreover, to the great disproportion between the height and diameter of plants, they are often surmounted by a heavy weight at the summit; the rye straw must sustain the burden of its ears of grain, the slender Palm the heavy and wind-swayed leaves (which in *Lodoicea Sechellarum* have a length of 7 m. and a breadth of 3-4 m.), while in the case of the *Cocos* palm the considerable weight of the bunches of fruit has also to be considered.

In plants, however, the rigid immobility of a building is not required, and they possess instead a wonderful degree of ELASTICITY. The rye straw bends before the wind, but only to return to its original position when the force of the wind has been expended. The mechanical equipment of plant bodies is peculiar to themselves, but perfectly adapted to their needs. The firm but at the same time elastic material which plants produce, is put to the most varied uses by mankind; the wood forms an easily worked yet sufficiently durable building material, and the bast fibres are employed for a variety of economic purposes.

In young stems and plants, in which the stiff but elastic wood and sclerenchymatous fibres are not developed, the necessary rigidity cannot be attained in the same way as in the older and woody stems. But although the principal component of such young stems is water (often 90 per cent or more), they maintain a remarkable degree of rigidity and elasticity through the elastic tension of their extremely thin and delicate cell walls.

Turgidity.—When air or water is forced, under pressure, into an elastic receptacle such as a rubber tube, the walls of the tube become stretched and the tube longer and thicker. By this process the tube becomes just so much stiffer and firmer the greater the internal pressure and the more elastic and thinner its wall. By the similar tension of their elastic cell walls arising from internal pressure, the rigidity and elasticity of thin-walled plant cells, and organs composed of them, are maintained. The cellulose walls of parenchymatous cells are, in spite of their delicate structure, exceedingly firm and, at the same time, elastic; when distended, therefore, by a strong internal pressure they exhibit physical properties similar to those of a rubber tube. In order to understand how such an internal pressure, actually existing within a cell, can arise, it is necessary to take into consideration the physical phenomenon of osmosis, first investigated by the botanist DUTROCHET, and later more particularly studied by PFEFFER and DE VRIES (2). Disregarding the recent and as yet merely theoretical views, according to which osmotic pressure, like that of steam, is supposed to be derived from the impact of motile, isolated molecules or ions against the walls, it will be assumed that osmosis is due simply to the mutual attraction of small particles of solid matter and their solvents. It depends also on the molecular attraction which converts solid bodies into solutions, and which so operates that the dissolved substances become uniformly distributed throughout the solution.

When two solutions of unequal concentration are separated by a membrane which is equally permeable to both, an attraction and diffusion of both liquids will take place through the separating membrane. If, however, the membrane is more easily permeated by one of the solutions than by the other, then a larger quantity of the one than the other will pass through it; and, in case the membrane is only permeable for one solution, that one alone will be drawn through it. If a pig's bladder be filled with a solution of common salt and then immersed in water, the flow of water into the bladder is more rapid than the outflow of the salt solution, and in consequence, an internal pressure is exerted within the bladder sufficient to expand it to a hard, rigid body.

A pressure similar to that arising from the osmotic attraction of the salt solution is produced in plant cells by the substances, particularly organic and inorganic acids, salts and sugars, held in solution in the cell sap. The living protoplasm of the cell does not allow any of the substances dissolved in the sap to pass out except such as escape through the diffusion taking place between the cells themselves. In this process a constant transmutation and transformation of the cell substances occurs, but, as may be observed in cells with coloured cell sap, these are held in by the protoplasm, and in particular by the protoplasmic membrane. These substances, however, draw in water through the cell walls and the protoplasm, and so set up a pressure within the cells often as high as 3-5 atmospheres. In some instances this pressure may amount to 10, 15, and 20 atmospheres (*e.g.* cells of the cambium and medullary rays of trees). Thus a tension is created which frequently exceeds that exerted by the steam of the most powerful locomotives. Through the force of such a tension the cell walls become so distended, that cells under the influence of this pressure or TURGIDITY become longer and larger than in their unexpanded condition.

When, from any cause, the quantity of water in such a turgescent cell is diminished the internal pressure is naturally decreased, and the cell walls, the distension of which may have amounted to 10-20 per cent, shrink together again. The cell grows smaller, and, at the same time losing its rigidity and elasticity, becomes soft and flaccid.

This condition occurs from natural causes when a succulent plant loses more water by evaporation than it can replace, and, in consequence, becomes flaccid. Such a flaccid plant plainly shows that the rigidity is not maintained by its framework of cell walls, but by the hydrostatic pressure within the cells, for with a more abundant water supply it returns to its original condition.

In addition to loss by evaporation, water is also withdrawn from cells by the same molecular force which causes the internal or endosmotic pressure. In cases where the cells are surrounded by a solution which exerts an attraction upon water, the turgidity of the cells is proportionally weakened, and, if the force of the exosmotic pressure is sufficient, it may be altogether overcome. On account of the consequent PLASMOLYSIS, or the contraction and separation of the protoplasm from the cell walls, occasioned by the withdrawal of water, the tension of the cell walls is decreased, and the cell becomes flaccid and collapses (Fig. 168), although completely surrounded by an aqueous solution.

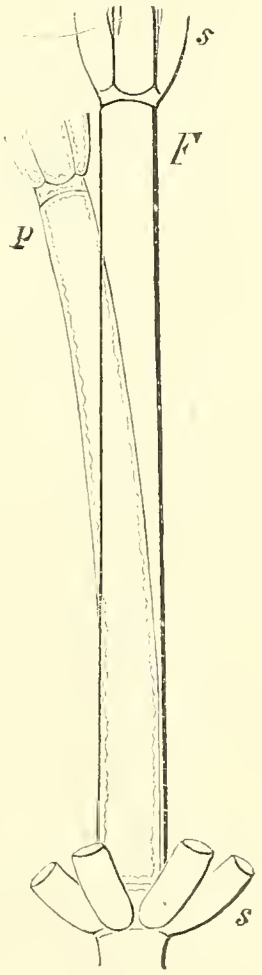


Fig. 168.—Internodal cell of *Nitella*. *F*, Fresh and turgescent; *p*, with turgor reduced, flaccid, shorter and smaller, the protoplasm separated from the cell walls in folds; *ss*, lateral segments. (× circa 6.)

If placed in pure water, however, the previous turgescence of the cells can be restored, that is, if their protoplasm has not been too strongly affected by the action of the solution. If the protoplasm has been killed in the process, it becomes permeable to water, and it is no longer possible to set up an internal pressure. Fresh sections of Beets or Carrots, placed in water, give up none of their sugar or colouring matter; but after the protoplasm has been killed, the sugar and colouring matter at once escape into the surrounding water, and the sections lose their firmness and rigidity.

On the other hand, Fungi or marine plants, when placed in a weaker saline solution or in fresh water, have the internal pressure of their cells increased. This may even lead to the rupture of the cell wall.

Through a knowledge of the strength of a solution necessary to produce plasmolysis, a means is afforded of measuring the internal pressure within plant cells. For example, if a solution of saltpetre with an osmotic pressure of 5 atmospheres (a 1 per cent solution, according to Pfeffer's investigations, gives rise to a pressure of about 3½ atmospheres) is just sufficient to overcome the turgidity of a plant cell (which in the case of stretched elastic cells shows itself by the limit of contraction being reached), then, conversely, the cell sap exerts upon water an equivalent endosmotic pressure. The force required to forcibly stretch a flaccid or plasmolysed organ to its original length furnishes also a rough means of estimating the pressure developed in turgescent tissues.

In the tension produced by turgidity we see how purely physical processes determine the rigidity of plants. These PHYSICAL processes are, however, dependent upon the VITAL functions of plants, inasmuch as they can only be called into action by living protoplasm. Living plant cells have thus power to regulate the physical effects of osmotic pressure by increasing or diminishing, or even suddenly overcoming their turgidity (cf. Movements of Irritability). It will also be apparent, in considering the operation of other physical forces, that the primary and essential result of the vital action is to give rise to the operation of physical processes, to favour, constrain, or vary them in such a way that they become of service to plant life.

Tension of Tissues.—The rigidity of parenchymatous tissue although to a large extent dependent upon the tension arising from the turgidity of its individual cells, is nevertheless considerably enhanced by the opposing pressure between the inner and outer tissue systems, in particular, between the pith and the epidermal and cortical tissues. The pith in this case represents the cell sap, as it is continually striving to increase its volume; the epidermal and cortical layers, on the other hand, by the pressure of the internal pith cylinders, are stretched and distended, just as are the cell walls by the osmotic pressure of the cell sap. The tension thus arising from the mutual resistance of different tissue systems acts upon the various plant organs like the turgidity of the single cells, and keeps them firm and rigid.

The tension of tissues is easily demonstrated by removing a strip of the peripheral tissue from a piece of a turgescent stem (of a Sunflower, *Helianthus*, for example), and cutting out the pith. It will be found that the outer tissue at once becomes shorter, and the pith longer than when they were both united in the stem. If the length of the stem experimented upon was 50 cm., the cortical strip would shrink to 46 cm., and the pith lengthen to 60-70 cm.

According to J. C. Müller a pressure of 13½ atmospheres would be needed to cause the isolated pith to resume its original length.

From this experiment it will be seen that the natural length of a stem represents the equilibrium maintained between the tendency of the pith to elongate and of the outer tissues to contract. The cortical tissue between the epidermis and the pith affords a transition between the two extremes of tension, the inner cell layers are compressed like the pith, and the outer layers stretched like the epidermis. The tension of tissues is also demonstrated by the fact that each strip of a fresh shoot which has been split longitudinally will curve outward, so that the pith forms the convex, the epidermis the concave side.

There is often a great difference in tension even between the outer and inner layers of the tissue of hollow organs, such as the stalks of a Dandelion (*Taraxacum officinale*), which, when split longitudinally, curl into helices of many turns, especially if placed in water. A tension exists wherever resistant and unequally strained tissues are in contact, and often occurs in parts of plants where it does not assist, as in the leaves and stems, in maintaining the rigidity of the plant body. Longitudinal and transverse tensions occur, particularly when, through secondary growth, newly formed growing tissues have to overcome the resistance of other tissues. In this way the primary and then the secondary cortex of trees become greatly stretched by the new cambial growth, so much so, that if a ring of bark be removed from a stem and then placed round it, a force of ten atmospheres is needed to make the edges meet; this was shown by an experiment of Krabbe.

In the meristematic tissues of growing points there is scarcely any perceptible tension, while, on the other hand, in regions which are in a state of elongation the tension of the tissues attains its highest limit. After an organ has completed its growth the elasticity of the cell walls and the turgescence of the cells decrease; and the tension of the tissues is therefore also diminished. The requisite rigidity is, however, provided for by special groups of cells with thickened and hardened walls, which thus constitute a firm framework for the other tissues similar to the bony skeleton of the higher animals.

Mechanical Tissues (Stereome) (3).—The supporting framework of plants is provided by the thick-walled elements of the wood, the thickened sclerenchymatous fibres of the fundamental tissue and the bast, and more rarely by groups of stone-cells. The resistance which these forms of tissue offer when the attempt is made to cut or break them affords sufficient evidence of their hardness, tenacity, and rigidity. Moreover, SCHWENDENER has been able to determine their mechanical value by means of exact physical experiments and investigations. According to such estimates, the sustaining strength of sclerenchymatous fibres is, in general, equal to the best wrought-iron or hammered steel, while at the same time their ductility is ten or fifteen times as great as that of iron. Just as the mechanical tissues of the internal framework of plants exhibit the physical properties most essential for their purpose, their arrangement, as SCHWENDENER showed, will also be found equally well adapted to the various ends in view, according as they may be required to withstand the strain of flexure, traction, or pressure. To withstand bending, and to offer the utmost possible resistance to it, a peripheral disposition of the rigid mechanical tissue is the most favourable.

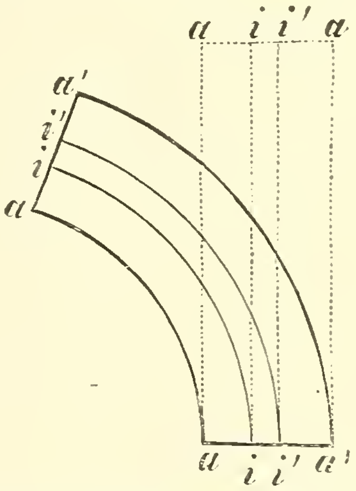


FIG. 169.—Longitudinal section of an elastic cylinder before and after curvature. Before curvature the peripheral (a, a') and central (i, i') vertical lines are of the same length (31·4 mm.). After curvature the peripheral line a' is 6·2 mm. longer; the other peripheral line a 6·3 mm. shorter. At the same time the central lines undergo but little change of dimensions.

When a straight rod (Fig. 169) is bent, the convex side elongates and the concave side contracts, that is, the outer edges (a, a and a', a') are exposed to the greatest variations in length, while, nearer the centre (i, i and i', i') the deflection and consequent variations in length are less. Accordingly, if the supporting skeleton of a plant stem be placed near the centre (i, i'), then a considerable degree of curvature is possible with but little flexure of the mechanical tissue. Nearer the periphery it would be subject to greater strain, and so offer a greater resistance to the deflecting force. In erect stems and flower-stalks, where rigidity is an essential requirement, the mechanical tissue is situated at the periphery, and often takes the form of projecting ridges

(Fig. 170, 1, 2). In roots, and in many rhizomes and stolons, as they must push circuitously between impeding obstacles, the skeleton system is central, as by this arrangement it is subject to less deflection, and can more effectually sustain strains upon its longitudinal elasticity (Fig. 170, 4). Fig. 170, 3 represents a transverse section through a band-like leaf of *Phormium tenax*, the New Zealand flax, which may reach a length of two metres ; it illustrates how such a leaf is strengthened by sclerenchymatous plates and strands. The mechanical elements of this leaf afford the strongest ships' cables.

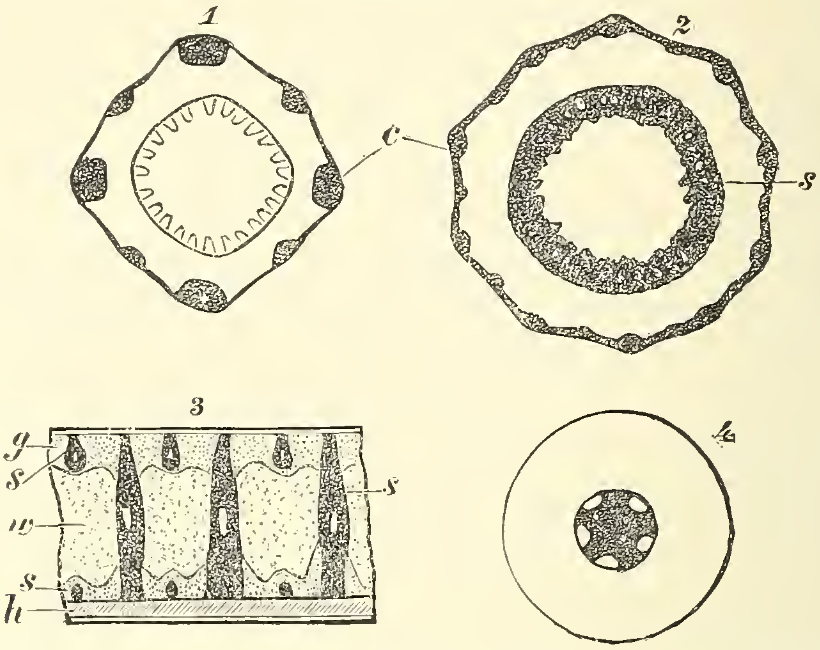


Fig. 170.—Disposition of mechanical tissue to secure rigidity. Transverse sections, 1, of a young shoot of *Sambucus* ; 2, of the floral shoot of *Eryngium* ; 3, of a leaf of *Phormium tenax* ; 4, of a root ; *c*, collenchyma ; *s*, sclerenchyma functioning as mechanical tissue (deeply shaded) ; *g*, green, and *w*, colourless leaf parenchyma ; *h*, hypoderma.

Where, however, pressure must be guarded against (as in Plum-stones, and in Hazel and Walnuts), the mechanical resistance is maintained by an arching mass of sclerotic cells, which, like sclerenchymatous fibres, are often further strengthened by deposits of mineral matter.

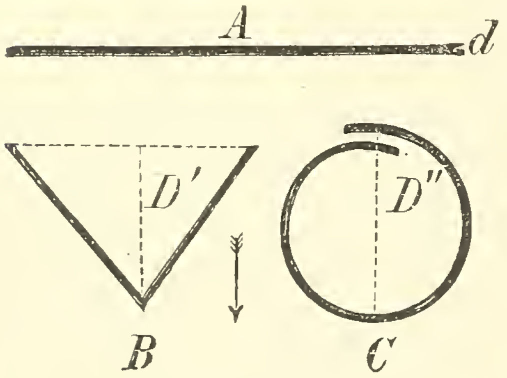


Fig. 171.—Diagrammatic transverse sections, to show method of securing rigidity by folding and rolling. In the outspread organ *A*, to withstand a pressure acting in the direction of the arrow, only the thickness *d* is available, but in the folded organ *B* the thickness *D'*, and in the rolled organ the thickness *D''*.

Stems of trees which have to support heavy and frequently large crowns, must, like pillars, be constructed to withstand pressure and bending.

All such heavily thickened, inflexible skeletal elements have lost their capacity for growth, and cannot, therefore, be utilised in those parts of plants which are in an actively growing state. In such cases where greater rigidity is required than can be maintained by cell turgidity and tissue tension, it is secured by the development of COLLENCHYMA (p. 67). This tissue, according to AMBRONN'S researches, in addition to its extreme resistance to tearing, possesses the power of elongating under the influence of the force of growth (4). The more capable it is of growth the more it responds to the growth in its neighbourhood. It forms, so to speak, the CARTILAGINOUS TISSUE of plants.

HEGLER (5) has shown that the plant is able to respond to a gradually increased demand by an increase in its rigidity due to the development of additional mechanical tissue.

Since, as has already been pointed out, the resistance of the mechanical elements to flexure is greater the farther they are removed from the centre of an organ, it will be readily seen that, while a flattened, outspread organ can be easily bent, if it were folded or rolled together, its power of resisting a deflecting force would be increased. In accordance with this principle many leaves become plaited or rolled (Fig. 171), and so acquire a sufficient rigidity without the assistance of any specially developed mechanical tissues.

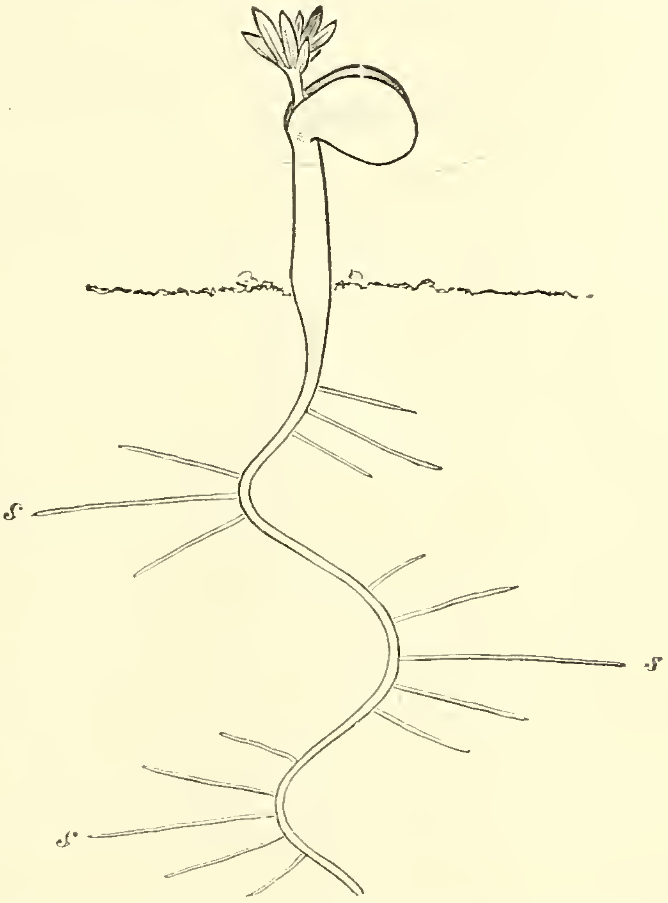


FIG. 172.—Young plant of Lupin, the main root of which has become curved. The lateral roots have arisen on the convex faces of the curves, and act as stays.

In addition to the rigidity of the individual organs of the plant, their arrangement and position are of importance for the stability of the whole organism. The lateral branches, which are normally arranged as symmetrically as possible, may be forced by bending them upwards or downwards to take on an elliptical cross-section or to form knee-like bends (6). The lateral roots originate from the convex flanks of a main root which has been thrown into curves (Fig. 172), and act as stays, preventing the straightening of the root and the loosening of the hold of the root-system, which would result from this (7).

II. Nutrition

By nutrition are understood all the processes of METABOLISM, or the chemical transformation and conversion of matter carried on by plants in the production and appropriation of their food-supply.

Without nourishment and without new building material no growth or development is possible. As the processes of elaboration and secretion are continuous, if the food-supply is not kept equal to the demands made upon it, the death of the organism from starvation must ensue, while a continuance of its growth and further development is only possible when there is a surplus of the elaborated food material.

The Constituents of the Plant Body.—By means of chemical analysis the constituent substances of plants have been accurately ascertained. It requires, however, no analysis to realise that a part, often indeed the greater part, of the weight of a plant is derived from the water with which the whole plant is permeated. Water not only fills the cavities of living, fully-developed cells, but it is also present in the protoplasm, cell walls, and starch grains. By drying at a temperature of 110°-120° C. all water may be expelled from vegetable tissues, and the solid matter of the plant will alone remain. The amount of dried substance in plants varies according to the nature and variety of the plant and of the particular organ. In woody parts it constitutes up to 50 per cent of their weight, but in herbaceous plants amounts to only 20 or 30 per cent. In more succulent plants and fruits it makes up only 5-15 per cent of their total weight; in water-plants and Algæ, 2-5 per cent, while everything else is water.

The dried substance of plants is combustible, and consists of organic compounds, which contain but little oxygen, and are converted by combustion into simple inorganic compounds, for the most part into carbonic acid and water. The elements CARBON, HYDROGEN, and OXYGEN form the chief constituents of the combustible dried substance. Next to them in quantity is NITROGEN, which is derived principally from the protoplasm. After combustion of the dried substance of plants there always remains an incombustible residue, the ASH, consisting of the mineral substances contained in the plant. As these mineral substances undergo transformation during the process of combustion, they are found in the ash in different chemical combinations than in living plants. From numerous analyses made of the ash of a great variety of plants, it has been determined that nearly all the elements, even the less frequent, are present in plants.

In addition to the four already named, the elements found in the ash of plants are sulphur, phosphorus, chlorine, iodine, bromine, fluorine, selenium, tellurium, arsenic (which may be combined as a superphosphate in the soil), antimony, silicon, tin, titanium, boron, potassium, sodium, lithium, rubidium, calcium, strontium, barium, magnesium, zinc, copper, silver, mercury, lead, aluminium, thallium, chromium, manganese, iron, cobalt, and nickel.

Many of these elements, indeed, occur only occasionally and accidentally, while others—sulphur, phosphorus, chlorine, silicon, potassium, sodium, calcium, magnesium, and iron—are met with in almost every ash. As might be inferred from the irregular occurrence of many of the elements, they are not all necessary for nutrition, and although their occasional presence in a plant may sometimes change certain of its special characteristics (thus the presence of zinc produces the so-called calamine varieties, such as, for example, *Thlaspi alpestre var. calaminare, Viola lutea var. calaminaria*, etc.), they do not exercise a decisive influence upon its existence.

The Essential Constituents of Plant Food.—Chemical analysis, while enabling us to determine the substances present in plants, does not show how far they are essential for nutrition. From culture experiments, in which the plants are grown in a medium of which the constituents are known, and kept under chemical control, it has been ascertained that, in addition to **carbon, hydrogen, oxygen,** and **nitrogen,** which form the principal part of the combustible elements of the dry substance of plants, **sulphur, phosphorus, potassium, calcium, magnesium,** and **iron** are absolutely indispensable to the growth of all green plants. In the absence of even a single one of these elements no normal development is possible.

According to MOLISCH, only nine of these elements are required by the *Fungi*. It is not, however, iron, as might be supposed, but calcium, that is unessential. On the other hand, the ten substances named suffice for the nutrition of most green plants; but it is not to be denied that certain other substances are of use in the plant economy and of advantage to growth, although not indispensable. Thus, for example, Buckwheat flourishes better when supplied with a chloride, and the presence of silica is advantageous as contributing to the rigidity of the tissues. It has also been discovered that by the presence of certain substances, in themselves of no nutritive value, the absorption of actual nutritive matter is increased (cf. p. 173). In the case even of the very poisonous copper salts, experience has taught that when they are brought into contact with the leaves (by sprinkling the plants with solutions to prevent the inroads of insects), they exercise a beneficial influence on the formation of chlorophyll, and increase assimilation, transpiration, and the length of life.

The nutritive substances are, naturally, not taken up by plants as elements, but in the form of chemical compounds. CARBON, the essential component of all organic substances, is obtained by all green plants solely from the carbonic acid of the atmosphere, and is taken up by the green leaves. All the other constituents of the food of plants are drawn from the soil by the roots. HYDROGEN, together with OXYGEN, is obtained from water, although the oxygen is derived also from the atmosphere and from many salts and oxides. NITROGEN is taken up by the higher plants only in the form of nitrates or ammonium salts; certain Fungi, Algæ, and carnivorous plants, however, obtain it in the form of peptone, amides, or even urea. As the ammonia of the soil formed by the soil bacteria (nitrite and nitrate bacteria, Stutzer's *Nitromicrobium*) from organic decaying matter is transformed by the help of other so-called nitrifying bacteria into nitrites, and eventually into nitrates, only the nitrogen combined in the nitrates need be taken into consideration (8).

Bacteria, as contrasted with the higher plants, are particularly characterised by their attitude towards nitrogen. In addition to the bacteria, which, by their nitrifying capability, are of service to green plants, there are other soil bacteria which set free the nitrogen of nitrogenous compounds and thus render it unserviceable for the nutrition of green plants. On the other hand, other forms of bacteria (e.g. *Clostridium Pasteurianum*) convert the free nitrogen of the air into compounds which serve not only for themselves, but also for the higher plants as convenient nitrogenous food material. From the comparison of the crops obtainable from plots of land with and without the addition of manure, J. Kühn has concluded that a very considerable fixation of nitrogen takes place in the soil (9).

Fig. 173.—Water-cultures of *Fagopyrum esculentum*. *I.* In nutrient solution containing potassium; *II.*, in nutrient solution without potassium. (After Nobbe, reduced.)

Sulphur and phosphorus form, like nitrogen, important constituents of protoplasm. All proteid substances contain sulphur. The sulphur is taken into plants in the form of sulphates; phosphorus in the form of phosphates. Potassium, unlike sodium, is essential to plant life, and is presumably active in the processes of assimilation and in the formation of protoplasm; it is introduced into plants in the form of salts, and constitutes 3-5 per cent of the weight of their dried substance. Magnesium, like potassium, participating in the most important synthetic processes of plants, is found in combination with various acids, particularly in reservoirs of reserve material (in seeds to the extent of 2 per cent) and in growing points (in leaves only ½ per cent). Calcium also is taken up in the form of one of its abundant salts, and in considerable quantities (2-8 per cent). Calcium plays an important part in the metabolic processes of plants, not indeed as an actual constituent of protoplasm, but as a vehicle for certain other essential substances, and, through its capacity to form compounds, as a means of fixing and rendering harmless hurtful by-products. IRON, although of the greatest importance in the formation of chlorophyll, is present in plants only in small quantities.

In order to determine the nutritive value of different substances the method of WATER-CULTURE has proved particularly useful (Fig. 173). In these culture experiments the plants, grown either directly from the seed or from cuttings, are cultivated in distilled water to which have been added certain nutritive salts. If all the essential nutritive salts are present in the culture solution, even larger plants, such as Indian Corn, Beans, etc., will grow to full strength and mature seeds as well as if grown in earth. It is not necessary in these experiments to provide carbon compounds in the nutrient solution, as plants do not derive their carbon supply through their roots, but, with the help of their leaves, from the carbonic acid of the atmosphere.

The young plants would grow for a time just as well in pure distilled water as in the nutrient solution; but as the supply of nourishment stored in the seeds became exhausted, they would gradually cease to grow, and die. If one of the essential constituents of plant food be omitted from the nutrient solution, although the young plants would grow better than in the distilled water, they would in time become abnormally developed. When, for example, a plant is grown in a nutrient solution containing all the essential food elements except iron, the new leaves developed are no longer green, but are of a pale yellow colour; they are "CHLOROTIC," and not in a condition to decompose the carbonic acid of the atmosphere and nourish the plant. Upon the addition, however, of a mere trace of iron to the solution the chlorotic leaves in a very short time acquire their normal green colour.

So long as the necessary nutritive substances are provided, the form in which they are offered to the plants, as well as the proportionate strength of the nutrient solution (if not too concentrated), may vary. Plants have the power to take up these substances in very different combinations, and are able to absorb them in other proportions than those in which they occur in the soil. In concentrated nutrient solutions the absorption of water is increased; conversely, in very dilute solutions it is the salts that are chiefly taken up. The presence also of certain substances often exerts an active and generally beneficial influence upon the capacity for absorbing other substances: thus, calcium salts increase the absorption of potassium and ammonium salts. In order to avoid the poisonous effects of phosphates and salts of iron, when supplied in a soluble form, v. D. CRONE (10) recommends the following nutritive solution:—

Distilled water	1-2 litres.
Potassium nitrate	0·5 gramme.
Ferrous phosphate	0·5 ,,
Calcium sulphate	0·25 ,,
Magnesium carbonate	0·25 ,,

A mixture of equal parts of ferrous phosphate and tri-calcic phosphate may be used in place of the ferrous phosphate in the above formula.

The phosphates which are present as a fine powder in the solution become deposited on the surface of the roots of plants growing in the fluid. Plants are found to grow better in the above solution than in those used by KNOOP and SACHS. The growth of Algæ is hindered in this solution.

As a most important result of such culture experiments, it has been demonstrated that only the ten elements already named are necessary for the growth of plants; all other elements, although present in plants in large quantities, are of subordinate value to plant life. This is true, for instance, of SODIUM, which in combination with CHLORINE actually predominates in some plants, and occasions the characteristic development of many of the succulent salt-plants; and also of SILICON, which, as silica, is so abundantly deposited in the cell walls of many plants—*Equisetaceae*, Grasses, Sedges, Diatoms (in the ash of Wheat-straw 70 per cent, and of *Equisetaceae* 70-97 per cent)—that, after combustion of their organic substances, it remains as a firm siliceous skeleton, preserving the structure of the cell walls. The hardness and firmness of the cell walls are so greatly increased by these siliceous deposits that some of the *Equisetaceae* are even used for polishing and scouring; while the margins of grass blades, from a similar deposition of silica in their cell walls, are often rendered sharp and cutting. The silicified cell walls of Diatoms occur as fossils, and form deposits of SILICEOUS EARTH (Kieselguhr) in some geological formations. The value of the siliceous concretions, termed "Tabasheer," that are found within the joints of Bamboo has not, as yet, been satisfactorily explained. ALUMINIUM, although like silica everywhere present in the soil, is only in exceptional instances taken up by plants. Aluminium has been detected in the ash of Lycopodiaceous plants; *Lycopodium complanatum* contains a sufficient quantity of acetate of aluminium to render the sap useful as a mordant. The same salt is found also in Grapes. On the other hand, although scarcely a trace of iodine can be detected by an analysis of sea-water, it is found, nevertheless, in large quantities in sea-weeds, so much so that at one time they formed the principal source of this substance.

The substances which, as culture experiments show, are not indispensable for the life of the plant, are, however, of use in so far as they can replace for some purposes (such as the neutralisation of free acids, etc.) essential elements of plant food. The latter are thus available for the special purposes for which they are indispensable. Thus K can be partially replaced by Na, and Mg by Ca.

It was first asserted by BERTHOLLET (1803), and afterwards emphasised by LIEBIG and C. SPRENGEL, that the mineral salts contained in plants, and once supposed to be products of the vital processes of the plants themselves, were essential constituents of plant food. Conclusive proof of this important fact was, however, first obtained by the investigations of WIEGMANN and POLSTORFF ([11]).

The actual proportions of the more important ash constituents of some well-known plants can be seen from the following table of ash analysis by WOLFF ([12]). The table also shows exactly what demands those plants make upon the soil, that is, what substance they take away from it, in addition to the nitrates which do not appear in the ash.

Plants.	Ash in 100 parts of dry solid matter.	100 Parts of Ash contain									
		K_2O	Na_2O	CaO	MgO	Fe_2O_3	Mn_3O_4	P_2O_5	SO_3	SiO_2	Cl
Rye (grain) . .	2·09	32·10	1·47	2·94	11·22	1·24	..	**47·74**	1·28	**1·37**	0·48
Rye (straw) . .	4·46	22·56	1·74	8·20	3·10	1·91	..	**6·53**	4·25	**49·27**	2·18
Pea (seeds) . .	2·73	43·10	0·98	**4·81**	7·99	0·83	..	**35·90**	3·42	0·91	1·59
Pea (straw) . .	5·13	22·90	4·07	**36·82**	8·04	1·72	..	**8·05**	6·26	6·83	5·64
Potato (tubers) .	3·79	60·06	2·96	2·64	4·93	1·10	..	16·86	6·52	2·04	3·46
Grape (fruit). .	5·19	56·20	1·42	10·77	4·21	0·37	..	15·58	5·62	2·75	1·52
Tea (leaves) . .	5·20	34·30	10·21	14·82	5·01	5·48	..	14·97	7·05	5·04	1·84
Coffee (beans) .	3·19	62·47	1·64	6·29	9·69	0·65	..	13·29	3·80	0·54	0·91
Tobacco (leaves)	17·16	29·09	3·21	36·02	7·36	1·95	..	4·66	6·07	5·77	6·71
Cotton (fibres) .	1·14	39·96	13·16	17·52	5·36	0·60	..	10·68	5·94	2·40	7·60
Spruce (wood) .	0·21	19·66	1·37	33·97	11·27	1·42	**23·96**	2·42	2·64	2·73	0·07

The great difference brought out by the table in the proportions of the more important phosphoric acid and of the less essential silica and lime contained in Rye and Pea seeds, as compared with the amounts of the same substances in the straw, is worthy of especial notice.

In a similar way the marine Algæ, according to WILLE (13), economise the nitrates and phosphates, which exist in small proportions in sea-water, but not potassium and magnesium, the supply of which is abundant.

In the preceding table the figures do not express absolutely constant proportions, as the percentage of the constituents of the ash of plants varies according to the character of the soil; thus, the proportion of potassium in Clover varies from 9 to 50 per cent; the proportion of calcium in Oats from 4 to 38 per cent.

The Process of Absorption (14).—As all matter taken up by plants must, as a rule, pass through continuous cell walls, it must be absorbed in a liquid or gaseous state. The only exception to this rule occurs in the amœboid forms of the lower plants (*Amœbæ* and Plasmodia), which, as they have no cell walls, are in a condition to take up and again extrude solid matter (particles of organic and inorganic substances).

The fact that plant cells are completely enclosed by continuous walls renders it necessary that food, to pass into the cell, must be either liquid or gaseous. In this condition the constituents of plant food are, however, imperceptible, and thus the manner of plant nutrition remained for a long time a mystery, and it was only during the eighteenth century that the nature of the nourishment and nutritive processes of plants was recognised.

Plant nourishment is dependent upon the permeability of the cell walls to liquids and gases. Although impervious to solids, the cell walls of living cells are permeated with "imbibed" water; and to this "IMBIBITION WATER" in the cell walls, together with the physical character of the cell walls themselves, are due their flexibility, elasticity, and ductility. The permeability of cell walls for imbibition water is only possible within certain limits, so that they thus retain the character of solid bodies.

Treated with certain chemical reagents (potassium hydrate, sulphuric acid, etc.) cell walls become swollen and gelatinous, or even dissolve into a thin mucilaginous slime. This change in their character is due to an increase in the amount of their imbibition water, induced by the action of the chemicals; otherwise, the water imbibed by ordinary cell walls is limited in amount. The walls of woody cells take up by imbibition about one-third of their weight; the cell walls of some seeds and fruits and of many Algæ absorb many times their own volume.

THE CELL WALLS ARE NOT ONLY PERMEABLE TO PURE WATER, BUT ALSO TO SUBSTANCES IN SOLUTION. This fact, that the cell wall offers no resistance to the diffusion of crystalloid bodies when in solution, is of the utmost importance to plant nutrition; cell walls, on the other hand, which are scarcely or not at all permeable to liquids (cuticularised walls), take no part in the absorption of plant nourishment, except in so far as they may still be permeable to gases.

In order that liquids may enter by osmosis into the living cell, they must first pass through the protoplasm, *i.e.* the lining of the cell wall. LIVING PROTOPLASM is not, however, like the cell walls, equally permeable to all substances in solution, but, on the contrary, COMPLETELY EXCLUDES CERTAIN SUBSTANCES, WHILE ALLOWING OTHERS TO PASS THROUGH MORE OR LESS READILY. Moreover, it is able to change its permeability according to circumstances, and thus THE OUTER PROTOPLASMIC MEMBRANE HAS THE POWER OF DECISION, whether a substance may or may not effect an entrance into the cell. Similarly the wall of the vacuole exercises a similar but often quite distinct power over the passage of substances from the protoplasm into the cell sap. The same determining power is exercised by these membranes in the transfer of substances in a reverse direction. On account of the selection thus exercised by the protoplasm, it is possible that, in spite of continued osmotic pressure, the contents of a cell are often of quite a different chemical nature from the immediately surrounding medium. To this same peculiar quality of the protoplasmic membranes is also due the SELECTIVE POWER of cells, manifested by the fact that different cells, or the roots of different plants, appropriate from the same soil entirely different compounds; so that, for instance, one plant will take up chiefly silica, another lime, a third common salt. The action of sea-weeds in this respect is even more remarkable; living in a medium containing 3 per cent of common salt, and but little potassium salts, they nevertheless accumulate much larger quantities of potassium than sodium. In addition they store up phosphates, nitrates, and iodine,—substances which are all present in sea-water in such small quantities as scarcely to be detected by chemical analysis. *Penicillium glaucum* is able to grow on a nutritive solution containing 21 per cent of sulphate of copper owing to the power it possesses of allowing the entrance to the cell of the necessary salts, while preventing that of the copper sulphate (15).

That osmosis may continue from cell to cell, it is essential that the absorbed material must become transformed into something else, either by the activity of the protoplasm or by some other means. Local accumulations of sugar or other soluble reserve material in fruits, seeds, bulbs, and tubers would otherwise not be possible; for osmotic action, if undisturbed, must in the end lead to the uniform distribution of the diffusible substances equally throughout all the cells. But if equilibrium is prevented by the transformation of the diffusible substances into others that are indiffusible, the osmotic currents towards the transforming cells will continue, and the altered and no longer diffusible substances will be accumulated in them. In this manner glucose passing into the cells of tubers or seeds becomes converted into starch. As a result of this a constant movement of new glucose is maintained towards these cells, which thus become reservoirs of accumulated reserve material.

Water and Mineral Substances

Without water there can be no life. THE LIVING PORTIONS OF ALL ORGANISMS ARE PERMEATED WITH WATER; it is only when in this condition that their vital processes can be carried on. Protoplasm, the real vehicle of life, is, when living, of a viscous, thinly fluid consistency, and when freed from its water either dies or becomes perfectly inactive.

The circumstance that protoplasm, when in a state of inactivity, as in spores and seeds, can often endure a certain degree of desiccation for a limited time, forms no exception to this rule. During such periods its actual vital functions entirely cease, and only renew their activity when water is again supplied.

In most plants desiccation occasions death, and it is always to be regarded as due to some special provision or exceptional quality when entire plants or their reproductive bodies can be again brought to life by a subsequent supply of water. Thus, for example, some Algerian species of *Isoetes*, and the Central American *Selaginella lepidophylla* can withstand droughts of many months' duration, and on the first rain again burst into life and renew their growth (16). In like manner many Mosses, Liverworts, Lichens, and Algæ growing on bare rocks, tree-trunks, etc., seem able to sustain long seasons of drought without injury. Seeds and spores, after separation from their parent plants, remain productive for a long time; seeds of *Nelumbium*, which had been kept dry for over one hundred years, proved as capable of germination as those of recent growth. A similar vitality was shown by moss spores which had lain in a herbarium fifty years. The often-repeated assertion concerning the germination of wheat found with Egyptian mummies ("mummy-wheat") has, however, been shown to be erroneous. Many seeds lose their power of germination after having been kept dry for only a year; others, even after a few days; and others again, as the seeds of the willow, cannot endure drying at all. On the other hand, the seeds of some water plants (*Eichhornia*, etc.) germinate better after being dried for a period ([17]). It must not be forgotten that in all these instances a certain amount of hygroscopic water is retained by plants even when the air is quite dry. Over the sulphuric acid of the desiccator, seeds retain for weeks 6 per cent or more of their weight of water. Even drying at 110° or the action of absolute alcohol can be borne by some spores and seeds.

Apart from permeating and energising the cells, water has other and more varied uses in plant life. It is not only directly indispensable for the solution and transportation of the products of metabolism, but also indirectly, in that its elements, hydrogen and oxygen, are made use of in organic compounds in plant nutrition. Water thus used (cf. p. 198) may be designated CONSTITUTION WATER; for example, in every 100 grammes of starch or cellulose there are 55 grammes of constitution water. It is also necessary for the turgidity and consequent rigidity of parenchymatous cells (p. 163); it is of use in the process of the growth of plant cells, which take it up in large quantities, and, through their consequent expansion, enlarge their volume with but little expenditure of organic substance.

A further and still more important service which water performs for plants consists in THE CONVEYANCE AND INTRODUCTION INTO THE PLANT BODY OF THE NUTRIENT SUBSTANCES OF THE SOIL. Although a large amount of water is retained in the plant body (up to 96 per cent in succulent tissues) for the maintenance of rigidity and enlargement of the organs, a still larger quantity of the water taken up by the roots passes through the plant merely as a medium for the transport of nourishment, and is again discharged through the leaves by evaporation. By this TRANSPIRATION from the aerial part of plants, the water passing into them from the roots escapes, and at the same time, by preventing saturation, which would otherwise be produced, tends to maintain a continuous upward movement of the water. The current of water thus produced is accordingly termed the TRANSPIRATION CURRENT. As the result of evaporation only water, in the form of vapour, and gases can escape from the plant. AS THE WATERY FLUID ABSORBED BY THE ROOTS CONTAINS SALTS, OXIDES, AND OTHER NON-VOLATILE SUBSTANCES IN SOLUTION, THESE ON EVAPORATION ARE LEFT IN THE PLANT AND GRADUALLY INCREASE IN QUANTITY. This accumulation of mineral salts is absolutely necessary for the plant, for the nutrient water taken up by the roots is so weak in mineral substances (it contains but little more solid matter than good drinking-water), that the plant would otherwise obtain too little food if it were only able to take up as much water as it could retain and make use of.

ALL THOSE CONTRIVANCES IN PLANTS, THEREFORE, WHICH RENDER POSSIBLE OR PROMOTE EVAPORATION, OPERATE CHIEFLY IN THE SERVICE OF NUTRITION. Were transpiration not in the highest degree useful and even necessary for the acquisition of mineral substances, provision would certainly have been made by plants to restrict it within the smallest possible limits. For transpiration increases the amount of water required by plants disproportionally to their powers of absorption, and exposes them, moreover, to the danger of perishing through the insufficiency of their water-supply.

In spite of the increased danger of drying up, as the result of evaporation, special provision is made by plants for facilitating transpiration (p. 187). To supply the increased demands for water thus produced there is set up a strong current of water containing nutritive salts in solution, which passes through the plants, and after yielding up its solid constituents, escapes in the form of invisible aqueous vapour. Thus plants, in order to obtain their nutrient substances, proceed in the same manner as some of the lower animals (Sponges, Ascidians), which draw in and maintain a continual flow of water through their bodies, in order to retain as food the nourishing particles suspended in it.

The Absorption of Water.—"Water," as here used, it must always be remembered, does not mean chemically pure water, but rather a DILUTE WATERY SOLUTION OF VARIOUS SUBSTANCES FROM THE ATMOSPHERE, FROM THE MINERAL SALTS OF THE EARTH, AND FROM ORGANIC HUMUS. In this connection it is also necessary to emphasise the fact that LIVING PLANTS DO NOT ABSORB THIS NUTRIENT WATER INACTIVELY AND INVOLUNTARILY, as a sponge, but through the peculiar selective power of their cells (p. 176) they exercise a choice from among the substances available.

The simpler and less highly developed plants, which are but slightly differentiated, are able to absorb water through the surface of their whole body. This is also generally true of all submerged aquatic plants, even of the Phanerogams. Water plants which obtain their nourishment in this way often either possess no roots (*Utricularia, Salvinia*), or their roots serve merely as mechanical hold-fasts. With plants living on dry land the conditions are quite different; their stems and leaves develop in the air, and they are restricted to the water held by capillarity in the soil. In order to obtain this water in sufficient quantities, special organs are necessary, which may spread themselves out in the soil in their search for water. These organs must absorb the water from the soil, and then force it to the aerial portions of the plant. This office is performed for a land plant by its root system, which, in addition to providing the supply of water, has also the task of mechanically sustaining the plant, and withstanding all influences which could lead to a disturbance of equilibrium by loosening the hold of the plant on the earth (18).

Conversely, loose soil is naturally bound together by the branching roots; and on this account plants have an economic value in holding together loose earth, particularly on dykes and land subject to inundation.

The small clod of earth, that is as a rule at the disposal of a plant in its natural habitat, is utilised to the full by the highly developed root system, which behaves in a wonderfully purposive manner.

If the development of the root system of a germinating Bean or Oak be observed, it will be found that the growing root of the embryo at once penetrates the soil and pushes straight downwards. Lateral roots are then given off from the main axis, and, growing either horizontally or diagonally downwards, penetrate the earth in the neighbourhood of the primary root. These lateral secondary roots in turn develop other roots, which radiate in all directions from them, and so occupy and utilise the entire soil at their disposal. The branching of the root system can proceed in this manner until, within the whole region occupied by the roots of a large plant, there is not a single cubic centimetre of earth which is not penetrated and exhausted by them.

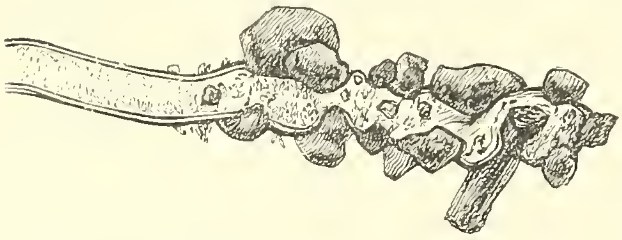


Fig. 174.—Tip of a root-hair with adhering particles of soil. (× circa 240.)

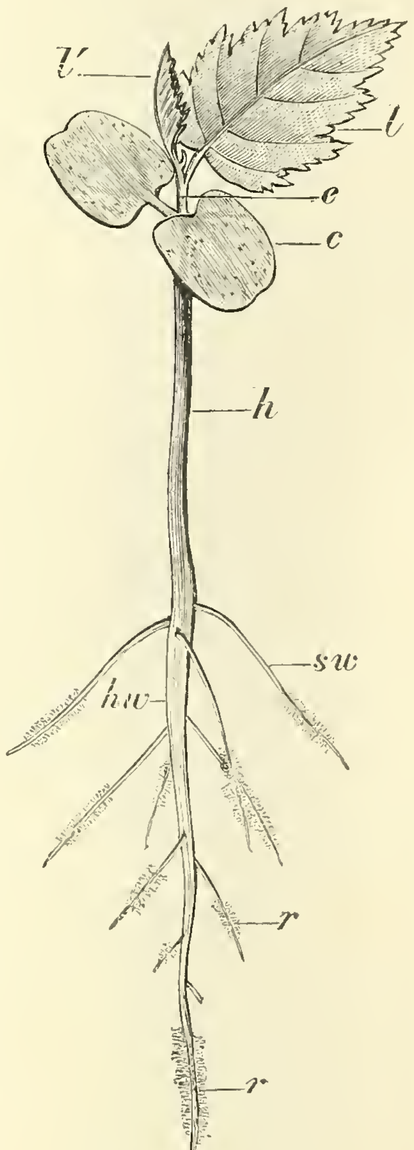


Fig. 175.—Seedling of *Carpinus Betulus*. *r*, Zone of root-hairs near root-tip; *h*, hypocotyl; *hw*, main root; *sw*, lateral roots; *l*, *l'*, leaf; *e*, epicotyl; *c*, cotyledons.

All plants do not form a deep-growing tap-root like that of the Oak, Silver Fir, Beet, Lucerne, etc.; some confine themselves to utilising the superficial layers of the soil by means of a thickly-branched lateral root system (Pine, Cereals). The agriculturist and forester must, accordingly, take into consideration the mode of branching and growth of the roots of a plant just as much as the habit of growth of its aerial portions. Plants which make use of different layers of soil may be safely cultivated together in the same soil, and succeed one another in the same ground. For similar reasons, in setting out trees along the borders of fields, the deep-rooted Elm should be preferred to the Poplar, whose roots spread out near the surface.

Desert or xerophilous plants, according to the observations of Volkens, send out deeply penetrating roots, which only branch profusely on reaching depths where they find water.

In order to secure a still more intimate contact with the particles of the soil, there are produced from the surface of roots small, exceedingly numerous, and fine cylindrical bodies, which penetrate the smallest interstices of the soil, and fasten themselves so closely to its smallest particles as to seem actually grown to them (Fig. 174). These ultimate branches of the root system, which discover the very smallest quantity of moisture, and seek out the most concealed crevices in their search for nourishment, are the ROOT-HAIRS,—delicate tubular outgrowths of the epidermal cells. Although they have the diameter of only a medium-sized cell, and appear to the naked eye as fine, scarcely visible, glistening lines, they often attain a length of several millimetres and enormously enlarge the absorbing surface of their parent root. According to F. SCHWARZ the epidermal surface of the piliferous zone of the roots of *Pisum*, which has 230 root-hairs to the square millimetre, is thus increased twelvefold.

The root-hairs do not cover the whole surface of roots, not even in the youngest roots, but only a comparatively small zone, a short distance above the growing root-tip. Soon after they have attained their greatest length, and have come into the closest contact with the earth particles, they die off. New root-hairs are developed to supply their place, so that a zone of root-hairs is thus constantly maintained just above the root-tip; while beyond this advancing zone of hairs the root epidermis becomes again completely divested of root-hairs (Fig. 175).

The older parts of roots, even in plants which persist for many years, take no part in the process of absorption. They envelop themselves with cork, increase their conducting elements by growth in thickness, and function exclusively in the transfer of the water absorbed by the younger portion of the roots. Even in the young roots the absorption seems principally confined to the regions covered with root-hairs, or, in case no root-hairs are developed, to a corresponding zone of the root epidermis.

Through the intimate union of the youngest roots with the soil, they are able to withdraw the minute quantity of water still adhering to the particles of earth, even after it appears perfectly dry to the sight and touch. There still remains, however, a certain percentage of water, held fast in the soil, which the roots are not able to absorb. Thus, SACHS found that the water left by a Tobacco plant, and which it could not absorb, amounted in cultivated soil to 12 per cent, in loam to 8 per cent, and in sand to 1½ per cent. Plants may even obtain a certain quantity of water from soil which is frozen hard.

The absorptive power of soil depends, partly, upon chemical changes taking place within it, but partly also on physical processes (the superficial adhesive force of its particles). The chemical changes are especially concerned with the retention of ammonium and potassium salts, as well as phosphates; the former as difficultly soluble silicates or double silicates, while phosphoric acid is held in combination with calcium or iron. Magnesium and calcium salts are, on the contrary, but slightly absorbed. They are, like the chlorides, the nitrates, and, in part, also the sulphates, easily displaced; in soil treated with a solution of saltpetre, for example, the potassium will remain in combination in the soil, while calcium nitrate passes off in solution.

Humus acids contribute, to a certain extent, to the chemical changes occurring in soil, as do also soil bacteria, which possess strongly oxidising and reducing powers (cf. p. 172).

The absorptivity of the soil, which, moreover, is not absolute, and varies with different soils (sandy soil absorbs poorly), operates advantageously for plants by the consequent rapid accumulation of large supplies of food-material for their gradual absorption.

The absorptive power of soil for water is due to its capacity to retain water by capillarity, so that it does not run off. Of the soils investigated by Sachs, cultivated soil retained in this way 46 per cent, loam 52 per cent, and sand only 21 per cent of water.

The activity of the roots in providing nourishment is not only manifested in overcoming the adhesive and absorptive power of the soil. The young roots, and especially the root-hairs, in addition to the carbonic acid exhaled by them, which, no doubt, also aids in loosening the soil, excrete a stronger acid or acid salt, by means of which they dissolve otherwise insoluble substances. Roots growing upon a polished plate of marble will so corrode it that an etched pattern of their course and direction is thus obtained. By placing the roots upon litmus paper, it may be demonstrated that the corrosion is due to the action of an acid.

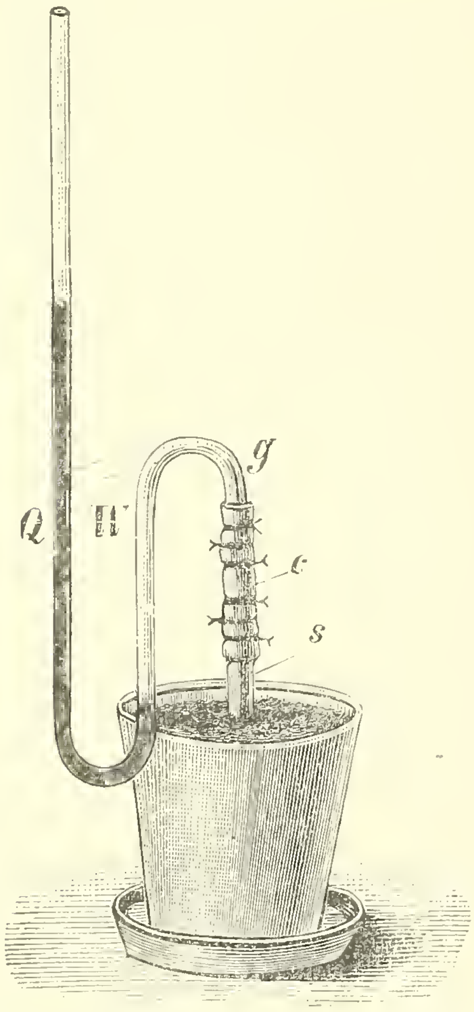


Fig. 176.—Vigorous exudation of water as the result of root-pressure from a cut stem of *Dahlia variabilis*. The smoothly cut stem *s* is joined to the glass tube *g* by means of the rubber tubing *c*. The water *W*, absorbed by the roots from the soil, is pumped out of the vessels of the stem with a force sufficient to overcome the resistance of the column of mercury *Q*.

The nutrient water with which the cell walls of the epidermal cells and root-hairs first become permeated is taken up by the epidermal cells, and thence passes through the cortical cells and the endodermis (p. 114) to the central cylinder of the root.

The Distribution of the Nutrient Water—1. Root-Pressure.—The causes which determine the direction and strength of the movement of the water through the living cells of the root-cortex into the vascular bundles are not yet fully understood. The fact that the water does actually pass into them, and at times indeed is forced into them with a considerable pressure, may be easily demonstrated. If the stem of a strongly-growing plant be cut off close above the ground, and the cut surface dried and then examined with a magnifying-glass, water will, in a short time, be seen to exude from the severed ends of the bundles. By close inspection, it is also possible to determine that the water escapes solely through the vascular or woody portion of the bundles. When the soil is kept warm and moist the outflow will be greater, and will often continue for several days. During this time, a half-litre or more of water will be discharged. This water, as analysis shows, is not pure, but leaves on evaporation a residue of inorganic and organic substances.

Again, if a hollow glass tube be placed on the root-stump and tightly fastened by rubber tubing, the exuded fluid will be forced up the glass tube to a considerable height. How great the force of this pressure is may be shown by attaching to the stump a manometer (Fig. 176). The column of mercury will in some cases be forced to a height of 50 or 60, and under favourable conditions to 100 or more centimetres, thus indicating a root-pressure which may sometimes considerably exceed one atmosphere, and is of sufficient power to raise a column of water 6, 8, and 18 metres high. In *Schizolobium excelsum* in Java, FIGDOR found a pressure of eight atmospheres. The height to which the fluid can be raised is the less surprising when the much greater forces due to turgescence, which are at the disposal of living cells, is remembered (19).

If, instead of the effects of the pressure, the volume of water exuded each hour be observed, the remarkable fact will be demonstrated that the roots regularly discharge more water at certain hours than at others (PERIODICITY OF ROOT-PRESSURE).

When it was shown that the roots were capable of exercising so great a pressure, it was at first believed that the ascent of the sap to the tops of the highest trees was due to root-pressure. This, however, would be impossible in view of the following considerations. The volume of water supplied by root-pressure is not sufficient to satisfy the quantity given off by evaporation. On the contrary, during moderately vigorous transpiration, such as takes place on a summer day, the root-pressure is of a negative character. Thus, if an actively evaporating plant be cut off near the root, no outflow of water will take place. On the other hand, the stump will energetically draw in water supplied to it; and not until it has become saturated does the force of the root-pressure make itself apparent. In plants growing under natural conditions, the root-pressure is only effective on damp, cool days, or at nights, when the transpiration is greatly diminished. In spring, when the roots are beginning their activity, the conditions are most favourable, the wood is full of water, and the transpiring leaves are not yet unfolded. When the wood is injured, "sap" is exuded in drops from the vessels and tracheids.

The so-called BLEEDING from wounds or cut stems is chiefly due to root-pressure, but it is also augmented by the pressure exerted by the living cells of the wood (wood parenchyma, medullary rays). FOR THE LIVING CELLS OF ALL OTHER PARTS OF THE PLANT LIKE THOSE OF THE ROOT ARE UNDER CERTAIN CONDITIONS ABLE TO FORCE OUT FLUID. The stimulus due to wounding may directly contribute to this (inflorescences of Palms, according to MOLISCH). The outflowing sap often contains, in addition to numerous salts, considerable quantities of organic substances (dissolved albuminous matter, asparagin, acids, and especially carbohydrates). The amount of saccharine matter in the sap of some plants is so great that sugar may be profitably derived from it. The sap of the North American sugar maple, for example, contains from 2 to 3½ per cent of sugar, and a single tree will yield 2-3 kilos. The sap of certain plants is also fermented and used as an intoxicating drink (palm wine, pulque, a Mexican beverage made from the sap of the Agave, etc.).

The bleeding which takes place on warm, sunny winter days from wounds or borings in trees is not due to root-pressure, but to purely physical causes. It is brought about by the expansion of the air-bubbles in the tracheal elements of the wood, and may be artificially produced at any time in winter by warming a freshly-cut piece of wood; when the wood is allowed to cool, the air contracts and the water in contact with the cut surface will be again absorbed.

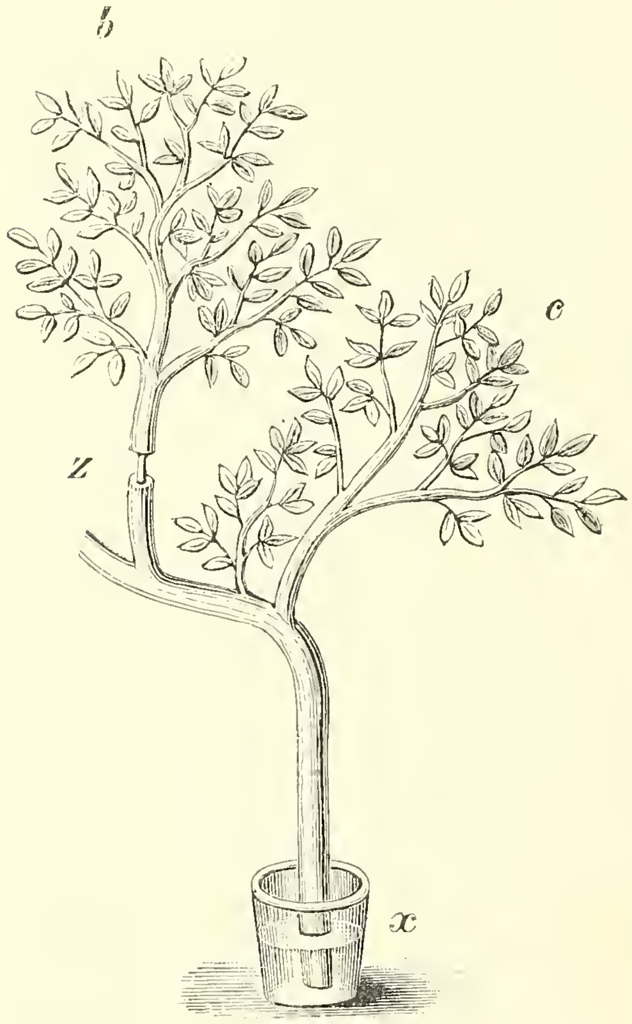


FIG. 177.—HALES' experiment to show the ascent of the sap in the wood. Although the cortex has been entirely removed at *Z*, and the wood alone left, the leaves of the branch *b* remain as fresh as those on the uninjured branch *c*; *x*, vessel containing water. Facsimile of the illustration in HALES' *Vegetable Statics*, 1727.

II. THE WATER-CONDUCTION IN PLANTS.—In living plant-tissues the cells of which require more or less water for their growth, for the maintenance or augmentation of their turgidity, and to supply the water lost by transpiration, there is a constant transfer of water from one cell to another. This transfer between the adjacent cells takes place much too slowly to equalise the great amount of water lost by evaporation from the foliage of a tall tree. IN ORDER TO TRANSFER THE WATER, QUICKLY AND IN LARGER QUANTITIES, FROM THE ROOTS TO THE LEAVES, PLANTS MAKE USE, NOT OF THE LIVING PARENCHYMA, BUT OF THE WOODY PORTION OF THE VASCULAR BUNDLES. The woody elements which thus conduct the water have no protoplasm.

III. THE TRANSPIRATION CURRENT.—It has long been known that the ascending transpiration current in woody plants, which is directed to the points of greatest consumption, flows solely through the wood. It had been observed that plants, from which portions of the cortex had been removed, either purposely or accidentally, remained nevertheless perfectly fresh. The adjoining figure, taken from one of the first books in which the vital processes in plants were accurately described (ESSAYS ON VEGETABLE STATICS, by STEPHEN HALES, 1727), shows the method employed in proving this fact experimentally (Fig. 177). At *Z* in the branch *b* all the tissues external to the slender wood have been removed. Since the leaves of this branch remain as fresh as those of the branch *c*, it is evident that the transpiration current must pass through the wood and not through the cortical tissues. On the other hand, when a short length of the wood is removed from a stem, without at the same time unduly destroying the continuity of the bark, the leaves above the point of removal will droop as quickly as on a twig cut off from the stem. It has also been shown by experiment that in herbaceous plants the vascular portions of the bundles provide for the conduction of the ascending currents.

As SACHS demonstrated by spectroscopical analysis, a dilute solution of lithium nitrate taken up by an uninjured plant first ascends in the wood before it passes laterally into the other tissues. By means of the same solution, MACNAB, PFITZER, and SACHS determined the velocity of the movement of the transpiration current, which naturally varies according to the plant and the effect of external conditions upon transpiration; under favourable circumstances it attains a rate of 1-2 metres an hour. The method of showing the exclusive share of the wood in the conduction of the water, and, also, of determining the maximum velocity of the transpiration current, from observations based on the path and rate of movement of a coloured solution taken up by a plant, is not free from objection; for the colouring matter would not pass through the stem at the same rate as the water in which it is dissolved, but would be drawn out and held back by the cells. The employment of coloured solutions will, however, be found instructive for merely showing the course of the transpiration current. The transparent stems of the Balsam, *Impatiens parviflora*, and the white floral leaves of Lilies, Camellias, Mock Orange, etc., in which the coloured vascular system will stand out as a fine network, are especially adapted for such an experiment.

In water plants and succulents, in which little or no transpiration takes place, the xylem is correspondingly feebly developed. In land plants, on the other hand, and especially in trees with abundant foliage, the wood attains a much greater development. All the wood, however, of a large stem does not take part in the task of water-conduction, but only the younger, outer rings. Where there is a distinction between heart- and sap-wood, under no conditions does the heart-wood take part in the conduction of the water, which is transferred exclusively by the younger rings of the sap-wood.

The character of the forces which cause the ascent of the transpiration current is still unexplained. Transpiration itself makes a place for the inflowing water. By the removal of the imbibition water from the cell wall, which is replaced at the expense of the supply contained in the osmotically active cell, force is exerted which causes the water in the adjacent elements of the xylem to move onwards. It is, however, doubtful whether this slight initial disturbance of the condition of equilibrium is sufficient, even when the cohesion of the water is taken into account, to account for the rapidity of movement and the distance covered by the transpiration stream. A sufficient and generally accepted explanation of this much-debated question is still wanting (^{20}).

It has been already explained that the ROOT-PRESSURE cannot exert such a force during transpiration (p. 183).

OSMOTIC FORCES act too slowly to be of any value, and, moreover, there is no fixed distribution of osmotic substances that would account for such a current.

The transpiration current cannot be due to CAPILLARITY. In the first place, continuous capillaries are entirely wanting in some plants (the Conifers, for example), and in the stems of others they are only present for comparatively short distances. Secondly, the concave menisci in the elements of the wood are not in relation with any level or convex surface of water, in which case alone they could have effect. Thirdly, the height to which liquids can rise by capillary attraction, and it would be less in the vessels and tracheids than in a glass tube, does not approach the height of an ordinary tree; and, finally, the rate of ascent induced by capillarity decreases so greatly with the increasing height of the fluid, that so copious a flow of water as occurs in plants would be impossible.

ATMOSPHERIC PRESSURE has, also, been shown not to be the cause of the transpiration current. In fact the vessels and tracheids of vigorously transpiring plants contain rarefied air between the short columns of water. This is evident from the way in which stems cut under mercury become penetrated by it. But as the water-courses in plants are all completely shut off from the outer atmosphere, the external atmospheric pressure could have no effect. The rarefied air within the plants, moreover, shows no such regularity in its distribution that it could possibly give rise to so continuous a flow of water. Further, as the atmospheric pressure can only sustain the weight of a column of water 10 m. high, while the sap rises in *Wellingtonia* 100 m. high and in *Eucalyptus* trees of the height of 150 m., the inadequacy of the atmospheric pressure to give rise to such a movement must be admitted.

The supposition that the water ascends in the form of vapour through the cavities of the wood, and is afterwards condensed in the leaves, is untenable, as is at once obvious from a consideration of the anatomical structure of the wood, the interruption of its cavities by short columns of water, and the temperature of the plants themselves. And, moreover, the special task of the transpiration current, to transfer the nutrient salts, could not be accomplished if such a supposition were true.

It has also been suggested that all of these processes might be aided by THE CO-OPERATION OF THE LIVING CELLS which are so abundant throughout the wood, and which have command of active osmotic forces, to the service of which they could unite a regulative irritability. STRASBURGER'S investigations, however, have shown that poisonous solutions, which would at once kill all living protoplasm, can be transported, in great quantities, to the summits of the loftiest Oaks and Firs. Thus the supposition that the living elements in any way co-operate in the ascent of the transpiration current is absolutely precluded.

Recently JOLY, DIXON, and ASKENASY have endeavoured to explain the transmission of the suction force of transpiration to the most distant root-tips by the fact of the cohesive force of the water. The occurrence of bubbles of air and vapour in the conducting channels, and the fact that movement of the water interferes with the power of its cohesive force to resist a pull are among the objections to this theory (21).

The most recent investigations agree in concluding that THE TRANSPIRATION CURRENT ASCENDS IN THE CAVITIES OF THE WOOD THROUGH THE VESSELS AND TRACHEIDS.

IV. SUCTION IN TRANSPIRING SHOOTS.—A shoot, the cut end of which is placed in water, shows by remaining fresh that it must be able to draw up water to its extreme tips. The force of suction exerted by such a transpiring foliage shoot may be demonstrated, by fitting the cut end in a long glass tube filled with water in such a manner that it shall be air-tight. Thus arranged, the shoot will be able to sustain and raise a column of water 2 metres high. If the lower end of the tube be inserted in mercury, as shown in the adjoining figure (Fig. 178), it will be found that even the heavy mercury will be lifted by the transpiring shoot to a considerable height. Vigorous coniferous shoots absorb water through the cut end with a force of suction equal to one atmosphere, and are thus able to raise the mercury to a height equal to the barometric pressure (760 mm.), and owing to the cohesion of the water column even beyond this (920 mm.) The complete exclusion of the external atmosphere is absolutely requisite for the existence of such a suction-force, a condition actually fulfilled in the water-courses of plants (22).

The Giving-off of Water.—The requisite amount and essential concentration of the nutrient water supplied by the transpiration current are maintained only by the constant discharge of the accumulating water. This may occur in two ways, either more profusely by the evaporation of the water through the cell walls and the stomata in the form of vapour—that is, by transpiration—or less copiously and also less frequently by the actual exudation of drops of water.

I. TRANSPIRATION. — In their outer covering of cork, cuticle, and wax, plants possess a protection from a too rapid loss of water. A Pumpkin, with its thick cuticle and outer coating of wax, even after it has been separated from its parent plant for months, suffers no great loss of water. A potato or an apple is similarly protected by a thin layer of cork from loss of water by evaporation. The green organs of plants, on the other hand, as they are active in the processes of nutrition, and must be able to get rid of their surplus water in order to secure the proper concentration of their nutrient salts, make little use of such protective coverings. On the contrary, they are provided with

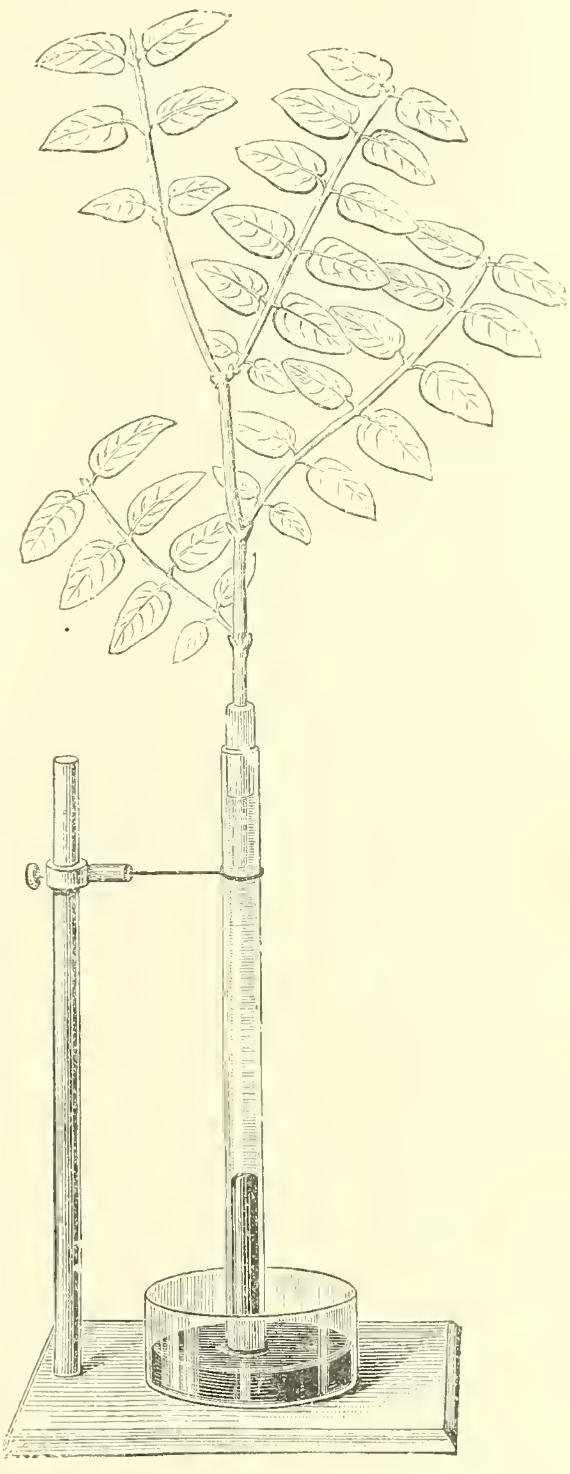


FIG. 178.—Suction of a transpiring shoot. The leafy shoot is fitted so that it is air-tight in a glass tube filled with water and the lower end immersed in a vessel of mercury. The mercury is drawn up the tube by the suction exerted by the transpiring shoot. (From DETMER'S *Physiol. Prakt.*)

special contrivances for promoting evaporation. The cell walls of all living organs are saturated with water, and, when the cuticle of the epidermis is not too strongly developed, water is constantly evaporated, even from uninjured cells, in amounts varying with the area of the exposed surfaces. From this point of view, it will be seen that THE FLAT EXPANSION OF FOLIAGE LEAVES RENDERS THEM ADMIRABLY ADAPTED FOR THE WORK OF TRANSPIRATION. Evaporation is also promoted by the numerous STOMATA (AIR-PORES) which penetrate the epidermis, and which give the air, saturated with watery vapour, an opportunity to escape from the intercellular spaces. Although the stomata are so small (0·0006 mm. and less) that neither dust nor water can pass through them into the plant, they are usually present in such enormous numbers (p. 99) and so suitably distributed that their united action compensates for their minuteness. When it is taken into consideration that a medium-sized cabbage leaf (*Brassica oleracea*) is provided with about eleven million, and a Sunflower leaf with about thirteen million air-pores, it is possible to estimate how greatly evaporation must be promoted by these fine sieve-like perforations of the epidermis.

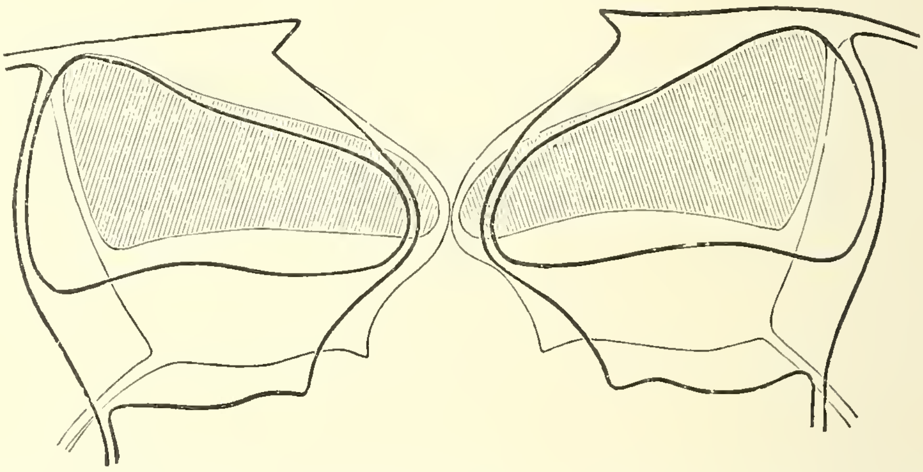


FIG. 179.—Stoma of *Helleborus sp.* in transverse section. The darker lines show the shape assumed by the guard-cells when the stoma is open, the lighter lines when the stoma is closed. (After SCHWENDENER.) The cavities of the guard-cells with the stoma closed are shaded, and are distinctly smaller than when the stoma is open.

The stomata also afford plants a means of REGULATING EVAPORATION. The pores, which are the mouths of intercellular spaces, are surrounded by GUARD-CELLS (p. 97). As the term guard-cell suggests, these cells have the power of closing the pore. THE CLOSING AND OPENING OF THE STOMATA ARE ACCOMPLISHED THROUGH A CHANGE IN THE TURGIDITY IN THE GUARD-CELLS. In consequence of their peculiar wall thickenings, elasticity, and lateral attachment, a change of turgidity affects the size and shape of the guard-cells in such a way that, by diminished turgidity, they become flatter and close the air-passage, while an increase of turgidity has the contrary effect and opens them (Fig. 179).

In many plants the so-called subsidiary cells (p. 98) participate in various ways and degrees in these processes, depending upon the special structure of the whole apparatus. The opening and closing of the stomata may be effected by either external or internal stimuli; but such stimuli affect different plants in a different manner. Generally speaking, the stomata begin to close on the diminution of the water-supply; they open, on the other hand, when active transpiration is advantageous (in light, in moist air, etc.). The quantity and quality of the substances held in solution in the nutrient water react in a remarkable manner upon the stomata. The size of their opening is decreased, and the quantity of water evaporated is therefore lessened when more than the usual amount of nutrient salts is present in the transpiration current; as in that case if, through continued evaporation, the nutrient water should become too concentrated, it might act disastrously upon the plant. In marsh and water plants the stomata react less promptly than in land plants (23).

It has already been pointed out, in describing the morphology of the stomata, that they are chiefly to be found on the surfaces of the leaves. THE LEAVES ARE ACCORDINGLY TO BE CONSIDERED AS SPECIAL ORGANS OF TRANSPIRATION (and assimilation, p. 195). This is also evident from the manner in which the vascular bundles branch after entering the leaves. As a large water-main divides into a network of smaller pipes where the consumption of the water takes place, so a leaf-trace bundle, after its long and uninterrupted course through the stem, suddenly branches as soon as it enters the leaf-blade. The adjoining illustration (Fig. 180), showing the nervature or distribution of the vascular bundles in a *Crataegus* leaf, will convey some idea of the extensive branching which the bundles of a leaf undergo, especially when it is taken into consideration that only the macroscopic and none of the finer microscopic branchings are represented in the figure. By means of this conducting system, a copious supply of nutrient water can be delivered directly from the roots to every square milli-

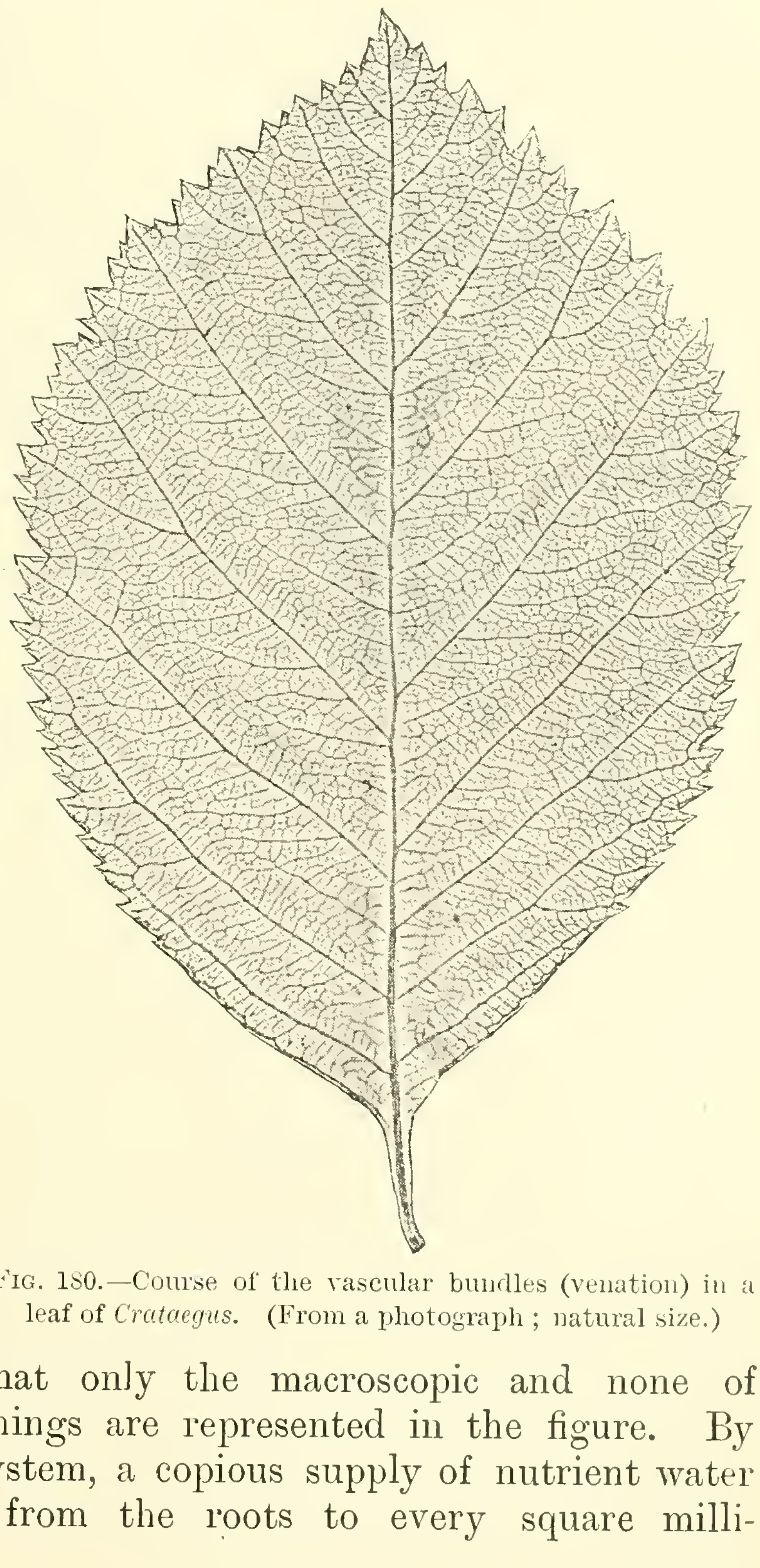


FIG. 180.—Course of the vascular bundles (venation) in a leaf of *Crataegus*. (From a photograph; natural size.)

metre of the leaf. There is, however, a special reason why the leaves are so abundantly supplied. They are the actual laboratories of plants, in which, out of the carbonic acid of the atmosphere and the water, and nutrient salts of the soil, the organic building material of the plant-body is produced. For similar reasons, it is in the leaves that the broad expansions of tissue for the special promotion of transpiration are found. The amount of water actually evaporated from the leaf surfaces in the performance of their vital functions is almost incredible. For instance, a strong Sunflower plant, of about the height of a man, evaporates in a warm day over a litre of water. It has been estimated that an acre of cabbage plants will give off two million litres of water in four months, and an acre of hops three to four millions. The quantity of water daily required to maintain the water-supply of a single large tree, amounts to many litres. For a Birch tree with about 200,000 leaves and standing perfectly free, VON HÖHNEL estimated that 400 litres of water would be lost by evaporation on a hot dry day; on an average the amount would be 60-70 litres. A hectare of Beech wood gives off on the average about 30,000 litres daily (^{24}).

It has been calculated that during the period of vegetation the Beech requires 75 litres and the Pine only 7 litres for every 100 grammes of leaf substance. According to DIETRICH, for every gramme of dry, solid matter produced, there is, on the average, 250-400 grammes of water evaporated.

EXPERIMENTAL DEMONSTRATION OF TRANSPIRATION.—The evaporation from plants, although imperceptible to direct observation, may be easily demonstrated, and its amount determined by the help of a few simple appliances. One method of doing this is to weigh a plant before and after a period of vigorous evaporation, and thus determine the amount of water actually lost. Or, if the water evaporated by a plant placed under an air-tight bell-jar be absorbed by calcium chloride or concentrated sulphuric acid, it will only be necessary to determine the increase in weight of the absorbing substance to estimate the amount of water given off by evaporation. The amount of water taken up by a plant may also be shown by so arranging the experiment that the water passes in through a narrow tube, as then even a small consumption of water will be quickly indicated by the rapid lowering of the water-level, which will be the more rapid the smaller the bore of the tube. Such a simple apparatus is called a potometer.

The important part taken by the stomata in the process of transpiration may be easily shown, according to STAHL, by means of the cobalt reaction, or the change in colour of dark-blue dry cobalt chloride to light rose upon absorption of water. In making this experiment a leaf placed between strips of paper which have been previously saturated with this cobalt salt and then thoroughly dried, is laid between glass plates. The paper on the side of the leaf most abundantly supplied with stomata will then first change its colour, and that too the more rapidly the more widely open are the stomata. This cobalt reaction, as also the iron and palladium chloride reaction used by MERGET, may be used to determine variations in the width of the stomatal openings. FR. DARWIN used a delicate hygrometer for this purpose in order to follow continuously the variations in width of the opening.

It is evident from these and similar experiments that more water is evaporated in a given time from some plants than from others. These variations are due to differences in the area of the evaporating surfaces and to structural peculiarities (the number and size of the stomata, presence of a cuticle, cork, or hairy covering, etc.). But even in the same shoot transpiration is not always uniform. This is attributable to the fact that, both from internal and external causes, not only the size of the openings of the stomata varies, but also that transpiration, just as evaporation from a surface of water, is dependent upon external conditions. Heat, as well as the dryness and motion of the air, increases transpiration for purely physical reasons; while light, for physiological reasons, also promotes it. From both physical and physiological causes, transpiration is much more vigorous during the day than night. Plants like *Impatiens parviflora*, which droop on warm days, become fresh again at the first approach of night.

II. Exudation of Water.—The discharge of water in a liquid state by direct exudation is not of so frequent occurrence as its loss by evaporation in the form of vapour. Early in the morning, after a damp night, drops of water may often be found on the young leaves of Indian Corn, and also on the leaves of *Alchemilla* and the Garden *Nasturtium*. These drops gradually increase in size until they finally fall off and are again replaced by smaller drops. These are not dew-drops, although they are often mistaken for them; on the contrary, these drops of water exude from the leaves themselves. They are discharged near the apex of the leaves of the Indian Corn, but in the case of *Alchemilla* from every leaf-tooth, and of the *Nasturtium* from the ends of the seven main nerves (Fig. 181). The drops disappear as the sun becomes higher and the air warmer and relatively drier, but can be produced artificially if a glass bell-jar be placed over the plant, or the evaporation in any way diminished. Whenever plants become overcharged with water through the activity of the roots, it is discharged in drops. These are pressed out of special water-pores (p. 99), and sometimes even from the stomata and clefts in the epidermis; while in *Datura* they have even been observed to exude directly through the walls of the epidermis. It is possible to cause similar exudations of water by forcibly injecting water into a cut shoot.

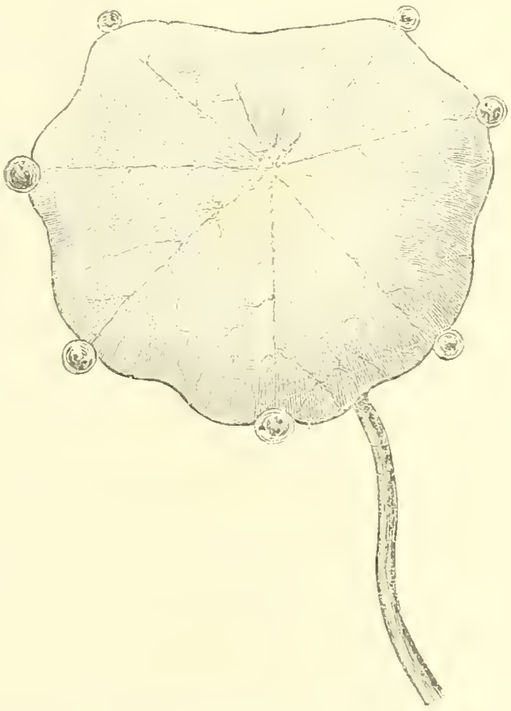


Fig. 181.—Exudation of drops of water from a leaf of *Tropaeolum majus*.

Such exudations of water are particularly apparent on many Aroids, and drops of water may often be seen to fall within short intervals, sometimes every second, from the tips of the large leaves. From the leaves of a species of *Colocasia* the exuded drops of water are even discharged a short distance. In *Spathodea*, a tropical member of the *Bignoniaceae*, the space enclosed by the calyx, in which the young floral organs are developed, is filled with water (25). Again, in unicellular plants, especially some of the Fungi (*Mucor*, *Pilobolus*, *Phycomyces*), the copious exudation of water is very evident. The water in this case is pressed directly through the cell walls.

The organs for the discharge of water, which HABERLANDT has collectively termed hydathodes (p. 102), in some instances, like animal sweat-glands, actively press out the water; or, on the other hand, they may simply allow it to filter through them when the internal pressure has attained a certain strength.

Since the excretion of water in the liquid form can occur when the conditions are unfavourable to transpiration (*Lathraea*), it may in a sense take the place of transpiration in maintaining the current from the water-absorbing organs (26). Its physiological significance is not, however, the same as transpiration, since the outpressed water always contains salts, and sometimes also organic substances in solution. In fact the quantity of salts in water thus exuded is often so abundant that after evaporation a slight incrustation is formed on the leaves (the lime-scales on the leaves of Saxifrages).

In some instances, also, the substances in solution in the water are exuded with a purpose, as in the case of the SECRETIONS OF THE NECTARIES and of the DIGESTIVE GLANDS OF INSECTIVOROUS PLANTS, and of the discharges of the viscid STIGMATIC FLUID. The excreted substances in these instances exert an osmotic attraction on the water in the cells of the plant; this distinguishes such cases from excretion dependent simply on the internal pressure. The substances excreted by some desert plants (*Reaumuria*, *Tamarix*) are so strongly hygroscopic that the leaves remain covered with numerous drops of liquid even in the dry air and under the arid conditions natural to the plants (27). The superfluous water is discharged by a few plants, the Pumpkin, for example, into the cavities of their stems and leaf-stalks, and is again absorbed from these reservoirs when needed.

Special Contrivances for regulating the Water-supply.—Almost all the higher plants possess in the power to close their stomata a special means of checking transpiration during a temporary insufficiency of the water-supply. In districts subject to droughts of weeks' or months' duration, only such plants can flourish as are able either to withstand a complete drying up without injury (p. 177), or to exist for a long time on a scanty supply of water. This last case is only rendered possible by the extreme reduction of transpiration, or by the formation of organs in which, in times of a superfluity of water, it may be retained for later use.

Such protection against excessive transpiration is afforded by the formation of cork or cuticular coverings, by the reduction in the number and size of the stomata, their occurrence in cavities or depressions, and the more or less complete filling of the opening by waxy substances. The rolling up of the leaves, as well as the development of thick growths of hair, or of a covering of star-shaped or scaly hairs, and the assumption of a vertical position to avoid the full rays of the sun, are also measures frequently adopted to lessen transpiration. The most efficient protection, however, from too great a loss of water by transpiration is undoubtedly obtained by the reduction of the transpiring surfaces, either through a diminution in the size of the leaves or through their complete disappearance.

The upright position of the leaves, or the substitution of expanded, perpendicularly directed leaf-stalks for the leaves (PHYLLODIA), particularly characterises the flora of Australia. A clothing of hair, on the other hand, protects the leaves of many South African *Proteaceae* (*e.g. Leucadendron argenteum*). Some of the *Gramineae* (*Stipa capillata, Festuca alpestris, Sesleria tenuifolia, S. punctoria*, etc.) roll or fold their leaf-blades, in times of drought, by means of special hinge-like devices, into narrow tubes, and so maintain a sufficient supply of water by diminishing the transpiration from their stomata. Reduction of the leaves is illustrated by the desert forms of *Genista* and *Sarothamnus* and by the Cypress-like Conifers. A complete disappearance of the whole leaf surface takes place in most *Cacti*, in which also the stems become swollen and converted into water-reservoirs (Fig. 28). A similar development of succulent swollen stems frequently occurs in the *Euphorbiaceae* (Fig. 182), in the *Compositae* (*Kleinia articulata*), *Asclepiadaceae*, and many other plant families found in arid regions. It has been estimated (^{28}) that the amount of water evaporated by a Melon-Cactus is reduced by its succulent development to $\frac{1}{6000}$ of that given off by an equally heavy climbing plant (*Aristolochia*). Instead of the stem the leaves themselves may become succulent, as in the House-leek and other species of *Sempervivum*, also in many species of *Sedum*, *Aloe*, and *Agave*. Both stem and leaves are equally succulent in many species of *Mesembryanthemum*. In other plants, the parenchyma of their stem tubers (epiphytic Orchids) or of their thickened roots (*Oxalideae*) serve as water-reservoirs. Epiphytic *Bromeliaceae* catch the rain-water in reservoirs formed by their closely-joined leaves, and then eagerly take it up through the scaly hairs which cover the leaf surfaces, as in species of *Tillandsia*. Again, many epiphytic Orchids and Aroids collect the rain-water in a swollen sheath developed from the epidermis of the aerial root (*velamen radicum*, p. 104). In the case of other epiphytic Orchids, Aroids, and Ferns (*Asplenium Nidus*, for instance), the humus and other material caught in receptacles formed by the leaves or aerial roots act like a sponge in taking up and retaining water, while th absorptive roots penetrate into these moist, compost-like masses and absorb both water and nutrient substances. Many species of *Frullania* (a Liverwort common on Beech trees) possess, on the other hand, special water-sacs on the under side of their thallus (Fig. 323). A particularly remarkable contrivance for maintaining a constant supply of water is exhibited by the epiphytic *Dischidia Rafflesiana*, a number of whose leaves form a deep but small-mouthed urn, into which the roots grow. It would seem at first sight unnecessary that plants like the Mangrove tree, which stand with their roots entirely in water, should require protection against too rapid transpiration; but, as this tree grows in salt or brackish water, it is necessary, as in other Halophytes, to reduce the amount of water absorbed, in order to prevent a too great accumulation of salt in the tissues.

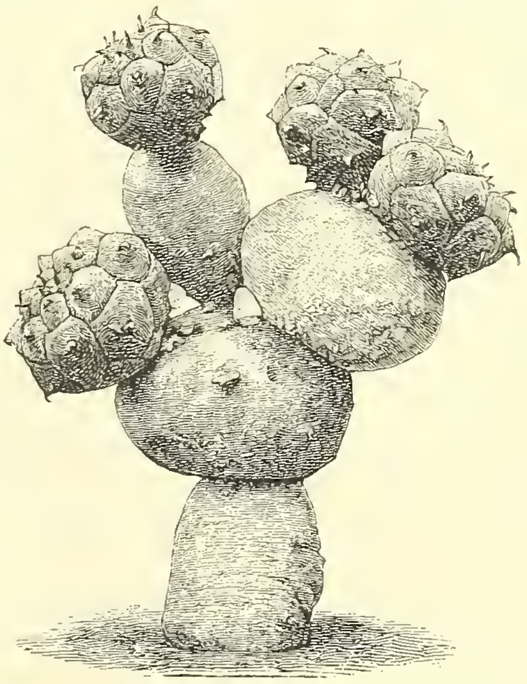


FIG. 182.—*Euphorbia globosa.* The reduced leaves may be seen on the upper globose shoots.

In high latitudes, where the soil remains frozen for months at a time, rendering the absorption of water by the plant difficult, arrangements are present to diminish transpiration similar to those found in desert plants (29).

The Absorption of Carbon (Assimilation)

In any attempt to distinguish the relative importance of substances utilised in plant nutrition, carbon undoubtedly ranks first. Every organic substance contains carbon, and there is no other element which could supply or take part in the formation of so many or such a variety of substances, both in living organisms and in the chemical laboratory. Organic chemistry, in short, is merely the chemistry of carbon compounds.

It requires no chemical analysis to realise that plants actually contain carbon, although in an imperceptible form. Every burning splinter of a match shows, by its carbonisation, the presence of this element. An examination of a piece of charcoal in which the finest structure of the wood is still distinguishable, shows how abundant is the carbon and how uniformly distributed. Estimated by weight, the carbon will be found to make up about half the dry weight (when freed from water) of the plant.

Whence do plants derive this carbon? The "humus" theory, accepted for a long time, assumed that the humus of the soil was the source of all the supply; and that carbon, like all the other nutrient substances, was taken up by the roots. That plants grown in pure sand free from humus, or in a water-culture, increase in dry substance, and consequently in carbon, clearly demonstrates the falsity of this theory. The carbon of plants must therefore be derived from other sources; and, in fact, the carbon in humus is, on the contrary, due to previous vegetable decomposition. The discovery made at the end of the eighteenth and the beginning of the nineteenth century, that THE CARBON OF PLANTS IS DERIVED FROM THE CARBONIC ACID OF THE ATMOSPHERE, and is taken up by the action of the green leaves, is associated with the names of INGENHOUSS, SENEBIER, THEO. DE SAUSSURE, and JUL. SACHS. This discovery is one of the most important in the progress of the natural sciences. It was by no means easy to prove that the invisible gaseous exchange between a plant and the atmosphere constitutes the chief source of nourishment; and it required the courage of a firm conviction to derive the thousands of pounds of carbon accumulated in the trees of a forest, from the small proportion (0·033 per cent) contained in the atmosphere.

The amount of carbonic acid gas contained in the air varies at different times and places. H. BROWN found that in 10,000 litres of air it was 2·7-2·9 litres in July, 3·0-3·6 litres in the winter; close to the ground 12-13 litres were present in the same volume. The average amount is about $3\frac{1}{3}$-$3\frac{1}{2}$ litres in 10,000 litres of the atmosphere. This weighs about 7 grammes, of which $\frac{8}{11}$ is oxygen, and only $\frac{3}{11}$ carbon. Accordingly, 10,000 litres of air contain only 2 grammes of carbon. In order, therefore, for a single tree, having a dry weight of 5000 kilos, to acquire its

2,500,000 grammes of carbon, it must deprive 12 million cubic metres of air of their carbonic acid. From the consideration of these figures, it is not strange that the discovery of INGENHOUSS was unwillingly accepted, and afterwards rejected and forgotten. LIEBIG was the first in Germany to again call attention to this discovery, which to-day is accepted without question. The immensity of the numbers just cited are not so appalling when one considers that, in spite of the small percentage of carbonic acid in the atmosphere, the actual supply of this gas is estimated at about 3000 billion kilos, in which are held 800 billion kilos of carbon. This amount would be sufficient for the vegetation of the entire earth for a long time, even if the air were not continually receiving new supplies of carbonic acid through the respiration and decomposition of organisms, through the combustion of wood and coal, and through volcanic activity. An adult will exhale daily about 900 grammes CO_2 (245 grammes C). The 1400 million human beings in the world would thus give back to the air 1200 million kilos of CO_2 (340 million kilos C). The CO_2 discharged into the air from all the chimneys on the earth is an enormous amount. CREDNER calculated that 460,000,000,000 kilos of coal are burnt annually, yielding to the atmosphere about 1,265,000 million kilogrammes of carbonic acid gas. The whole carbon supply of the atmosphere is at the disposal of plants, as the CO_2 becomes uniformly distributed by constant diffusion.

Not all plants, nor indeed all parts of a plant, are thus able to abstract the carbon from the carbonic acid of the air. Only such organs as are coloured green by chlorophyll are capable of exercising this function, for the chlorophyll bodies themselves are the laboratories in which this chemical process, so important for the whole living world, is carried on. From these laboratories is derived the whole of the carbon which composes the organic substance of all living things, plants as well as animals. Animals are unable to derive this most essential element of their bodies from inorganic sources. They can only take it up in organic substances, which have been previously formed in plants. Such plants, also, as are without chlorophyll, as, for example, the Fungi and some of the higher parasitic plants, are dependent for their nutrition upon organic substances previously formed by the chlorophyll bodies of other plants.

Roots and other organs unprovided with chlorophyll, and also the colourless protoplasm in the green cells themselves, are similarly dependent upon the activity of the chloroplasts.

The derivation of carbon from carbonic acid and its conversion into organic substances is termed ASSIMILATION. In its broadest sense, and especially in the animal kingdom, the word assimilation is used for all nutritive processes by which the nourishment is built up into the substance of an organism. But in Botany the meaning of the term has gradually been restricted, and now by assimilation the carbon assimilation of the chlorophyll granules alone is understood. Moreover, all the other so-called processes of assimilation are dependent upon carbon assimilation.

The chlorophyll bodies, however, cannot independently produce organic substances from carbonic acid and water, but require the co-operation of light (PHOTOSYNTHESIS). The chlorophyll apparatus is unable to assimilate without light, although all the other requirements are present for active assimilation. Given a source of illumination, either natural or artificial, assimilation commences, and, within certain limits, increases in proportion to the intensity of the effective rays. Unfavourable conditions, such as cold, or the presence of poisonous substances, may inhibit the action of the chlorophyll apparatus.

The vibrations of the ether perceptible as light, supply the energy for the decomposition of carbonic acid and the production of carbon, just as other vibrations, in the form of heat, supply the energy requisite for the working of a steam-engine. Not all light vibrations are equally capable of arousing the assimilatory activity. Just as the rays of different refrangibility differ in their action, both upon the eye and the photographic plate, so they have a different effect upon assimilation. It would be natural to suppose that the chemically active rays, the blue and violet, which decompose silver salts and other chemical compounds, would also be the most effective in promoting the assimilatory activity of the chlorophyll bodies. Exactly the contrary, however, has been shown to be the case. The highly refractive chemical rays have little or no effect on assimilation; the red, orange, and yellow rays, that is, the so-called illuminating rays of the spectrum, are on the contrary the most active (30).

In the red-leaved varieties of green plants, such as the Purple Beech and Red Cabbage, the chlorophyll is developed in the same manner as in the green parent species, but it is hidden from view by a red colouring matter in the epidermis: in the case of the brown and red Algæ, on the other hand, the chlorophyll pigment is concealed by a colouring matter, which is contained in the chromatophores along with the chlorophyll.

In the blue-green fresh-water Algæ, and also in the brown and red Seaweeds, in which the chromatophores contain true chlorophyll in addition to their peculiar special colouring matter, the maximum assimilation takes place, according to ENGELMANN, in another part of the spectrum than it does in the case of green plants. The assimilation in these Algæ seems indeed to be carried on in the part of the spectrum, the colour of which is complementary to their own (31). All the rays of the mixed white light are usually at the disposal of plants growing freely in the open air; only the Seaweeds found in deep water (at the most but 400 m. deep) grow in a prevailing blue light, while the deeper-lying tissues of land plants live in red light, as this penetrates further into the parenchymatous tissues.

In studying the effect of different kinds of light upon assimilation, it is customary either to use the separate colours of the solar spectrum, or to imitate them by means of coloured glass or coloured solutions. For such experiments it will be found convenient to make use of double-walled bell-jars filled with a solution of bichromate of potassium or of ammoniacal copper oxides. Plants grown under jars filled with the first solution, which allows only the red, orange, and yellow rays to pass through, assimilate almost as actively as in white light. Under the jars containing the second solution, which readily permits the passage of the photo-chemical rays, assimilation is extremely low.

But little is known with regard to the processes carried on in green cells during assimilation ; and although it is evident that only the green chlorophyll bodies are capable of assimilating, it is still by no means clear what part the green chlorophyll pigment performs. The pigment which may be extracted from the protoplasm of the chlorophyll bodies makes up only a small part of their substance (about 0.1 per cent), and gives no reaction from which its operations may be inferred. The light absorbed by the chlorophyll pigment also stands in no recognisable relation to the requirements of assimilation, for the assimilation is not proportional to the intensity of the absorption of the different rays. The proportion of the energy, passing through the leaf in the form of light, utilised in assimilation is, according to the thermo-electric measurements of DETLEFSEN, only 1 per cent ; according to the calculations of H. BROWN, ½ per cent in sunlight, and over 2 per cent in diffuse light (32). It has not as yet been determined what part the mineral constituents of the transpiration current take in the process. On the other hand, the protoplasmic body of the chloroplasts cannot assimilate when the green pigment is not present ; that is when, from any cause, the corpuscles are prevented from turning green. For, as the existence of the green pigment is dependent upon the presence of iron, of carbohydrates and other food substances, upon a proper temperature, and, with few exceptions (Ferns, Conifers, lower Algæ in culture solutions), upon the action of light, its formation in the chlorophyll bodies may be prevented by depriving them of the requisites for its development. The chromatophores will then remain yellow (in leaves) or white (in stems), and no longer assimilate.

Within recent years it has, indeed, been repeatedly determined that certain nitrifying bacteria have the power of forming a small amount of organic substances from carbonates, carbonic acid, and ammonia. The process by which the organic carbon compound is derived must, however, be altogether different from that of green plants, as the bacteria contain no chlorophyll, and their nutritive activity is in no way dependent upon the light. The necessary energy is here obtained not from photosynthesis but from the oxidation of ammonia into nitrous acid, and this into nitric acid (chemosynthesis). The formation of organic substance in the so-called purple bacteria is also insufficiently understood.

As a result of the chemical processes involved in the decomposing activity of assimilation, only the special end-product and one by-product are at present known. SACHS discovered that the organic compound, first to be detected as the special ultimate products of assimilation in the higher plants, is a CARBOHYDRATE, which may either remain in solution, or in the form of STARCH GRAINS may become microscopically visible at the points of its formation. In the case of the lower plants, in the Algæ, for example, the first visible product is often not starch but a fatty oil, protein, or some other secondary product.

A short time after assimilation begins, in sunshine, sometimes within five minutes, minute starch grains appear either in the centre or on the margins of the chloroplasts. These grains gradually enlarge until, finally, they may greatly exceed the original size of the chloroplasts. Should, however, the assimilation cease, which it regularly does at night, then the starch grains are dissolved and as soluble carbohydrates (glucose, etc.) pass out of the cell. In some plants (many Monocotyledons) there is no starch formed in the chloroplasts, but the products of assimilation pass in a dissolved state directly into the cell sap. In exceptional cases, however, starch is also formed where there is a surplus of glucose, sugar, and other substances, as, for example, in the guard cells of Monocotyledons. This seems then to be a reserve substance rather than a special product of assimilation. In *Tropaeolum*, for instance, the formation of cane-sugar precedes the production of starch in the chloroplasts.

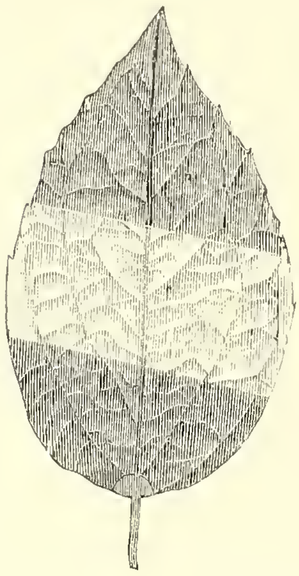


Fig. 183.—A leaf showing the iodine reaction. Part of an assimilating leaf was covered with a strip of tinfoil. Afterwards, when treated with a solution of iodine, the part of the leaf darkened by the overlying tinfoil, having formed no starch, gave no colour reaction. ($\frac{3}{4}$ nat. size.)

The formation of starch may be shown to be a direct result of assimilation by means of the "iodine reaction," and without the aid of a microscope. If a leaf cut from a plant previously kept in the dark until the starch already formed in the leaves has become exhausted, be treated with a solution of iodine after being first decolorised in hot alcohol, it will in a short time assume a yellowish brown colour, while a leaf vigorously assimilating in the light will, with the same treatment, take a blue-black colour. In Fig. 183 the result of the iodine reaction is shown on a leaf, part of which had been covered with a strip of dark paper or tinfoil. The cells darkened by the overlying paper or foil formed no starch, while those exposed to the light are shown by the iodine reaction to be full of it. A green leaf kept in air devoid of carbonic acid, although fully exposed to the light, will similarly form no starch.

The by-product arising from the assimilatory process is PURE OXYGEN. The volume of oxygen thus set free is nearly equal to the volume of carbonic acid taken in. If plants assimilate in a known quantity of air containing carbonic acid gas, its volume will therefore remain nearly the same. The chemical process of assimilation resulting in the decomposition of the carbonic acid may be thus expressed:

$$6CO_2 + 5H_2O = \underset{\text{(Starch)}}{C_6H_{10}O_5} + 6O_2$$

From this chemical equation (33) it is evident that WATER IS REQUISITE FOR THE PROCESS OF ASSIMILATION. The actual composition of starch corresponds rather to a multiple of the above symbol, or $n(C_6H_{10}O_5)$, so that the whole equation should be multiplied by n.

The oxygen given off by green plants, although not perceptible when they are growing in the open air, becomes apparent in the case of water plants. It was, indeed, through the evolution of bubbles of oxygen from water plants that INGENHOUSS first had his attention called to the assimilatory activity of leaves. To see this process, it is only necessary to place a cut stem of a water plant in a vessel of water exposed to the sunshine, when a continuous series of small bubbles of gas will at once be seen to escape from the intercellular passages intersected by the cut. The gas thus evolved may be collected with little trouble (Fig. 184), and will be found to be chiefly oxygen, but containing also traces of other gases derived by diffusion from the plant and the water. As water absorbs much less oxygen than carbonic acid (at a temperature of 14° C. 100 vols. of water will dissolve only 3 vols. of oxygen, but 100 vols. of carbonic acid), the escaping bubbles of oxygen become visible; whereas the flow of the carbonic acid dissolved in the water to the assimilating plant is imperceptible.

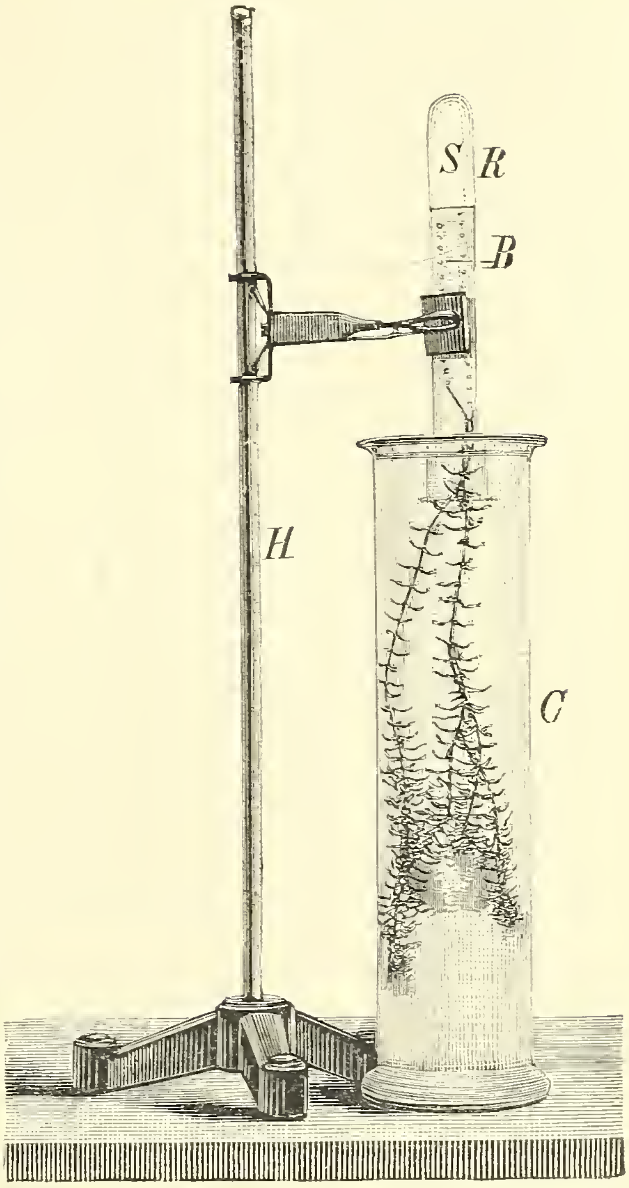


FIG. 184.—Evolution of oxygen from assimilating plants. In the glass cylinder *C*, filled with water, are placed stems of *Elodea canadensis*; the freshly-cut ends of the stems are introduced into the test-tube *R*, which is also full of water. The gas-bubbles *B*, rising from the cut surfaces, collect at *S*. *H*, stand to support the test-tube.

Artificially conducting carbonic acid through the water increases, to a certain degree, the evolution of oxygen, and thus the assimilatory activity. Similarly an artificial increase of carbonic acid in the air is followed by increased assimilation. According to KREUSLER assimilation in sunshine attains its maximum in air containing about 10 per cent of carbonic acid; with a higher percentage it begins to decrease. If the amount of carbonic acid gas be increased three hundred times (from 0.033 per cent to 10 per cent in the atmosphere), the formation of starch is only increased 4-5 times, while an increase of the CO_2 to six times the normal proportion results, according to H. BROWN, in the formation of six times as much starch (34).

Carbon monoxide (CO) cannot be utilised by green plants; it cannot take the place of the carbon dioxide, and is poisonous to plants, though less so than to animals.

Under the same external conditions, the assimilatory activity of different plants may vary from internal causes. In the same time and with an equal leaf surface, one plant will form more, and another less carbohydrates. In this sense, it is customary to speak of a "specific energy of assimilation," which is partly due to the different number and size of the chloroplasts, as well as to a difference in the air-spaces and consequent aeration of the leaves, but, without doubt, has also its cause in their greater or less energy.

As examples of medium assimilatory activity, the leaves of the Sunflower and Pumpkin may be cited. Under conditions favourable for assimilation, the leaves of these plants form in a summer day of fifteen hours about 25 grammes starch per square metre, while *Catalpa*, according to Brown, forms 1 gramme per hour and square millimetre of surface. The carbon for the formation of the starch was supplied in this case from 50 cubic metres of air. A room of 120 cubic metres would accordingly contain enough carbonic acid for 60 grammes of starch. From these figures a faint conception may be gained of the enormous activity of the assimilatory processes, which are necessary to furnish the yearly grain supply of a large country.

The Mechanism of Gaseous Exchange

The gaseous exchange between one of the lower plants (or a submerged Phanerogam) and the surrounding medium is carried on by diffusion through the whole surface of the plant. In a more highly organised plant the exchange takes place by means of the stomata. The escape of aqueous vapour and the entrance and escape of carbonic acid gas and oxygen in the processes of assimilation and respiration (p. 216) alike take place almost entirely through these openings. But in spite of their enormous number, the total area of the stomatal apertures is only about 1 per cent or less of the whole surface area, for each individual opening is very small (about 0·0001 sq. mm. in *Helianthus*). Brown and Escombe have, however, shown that the minuteness of the openings, combined with the peculiar distribution of the stomata, results in a greatly accelerated rate of diffusion. Diffusion through a number of fine apertures is much greater than through a single aperture of the same total area. When the small openings are placed about ten times their diameter apart the diffusion is nearly as rapid as when no separating wall is present. The distribution of the stomata in the epidermis very nearly meets these requirements. For example, a square millimetre of the surface of a *Catalpa* leaf absorbs about two-thirds the amount of carbonic acid gas taken up in an equal time by the same area of potash solution freely exposed to the air ([35]).

The Utilisation of the Products of Assimilation

The Formation of Albuminous Substances.—The chlorophyll bodies supply plants with organic nourishment in the form of a carbohydrate. Although the greater part of the organic plant substance consists only of carbohydrates, as, for example, the whole framework of cell walls, yet the living, and consequently the most important component of the plant-body, the protoplasm, is composed of albuminous substances. These albuminous substances have a composition altogether different from that of the carbohydrates. In addition to carbon, oxygen, and hydrogen, they also contain nitrogen, sulphur, and frequently phosphorus, the nitrogen indeed in considerable proportion (about 15 per cent). THERE TAKES PLACE ACCORDINGLY WITHIN PLANTS A NEW FORMATION OF ALBUMINOUS SUBSTANCES

FROM THE CARBOHYDRATES. There are certain indications that this formation is, in part, accomplished within the green cells of the leaves, but it must also be carried on in cells devoid of chlorophyll, as, for instance, in those of the Fungi.

As little is known concerning the process of the synthesis of the albuminous substances of plants as concerning the formation of the carbohydrates from the carbonic acid and water. It has generally been supposed that they are formed from the carbohydrates and mineral substances already mentioned, as these are known to be transported to the region where the formation of protoplasm occurs, and are there consumed. The carbohydrates utilised in this process seem to be principally GLUCOSE (both grape-sugar, dextrose, $C_6H_{12}O_6 + H_2O$, and fruit-sugar, lævulose, $C_6H_{12}O_6$) and MALTOSE ($C_6H_{22}O_{11} + H_2O$); for, whatever may be the form of the original carbohydrate, whether starch, inulin, cane-sugar, reserve-cellulose, or glycogen, glucose or maltose is always the first product formed from it.

The mineral nitrates, sulphates, and phosphates take part in the process, chiefly in the form of potassium and magnesium salts. Nitrogen and sulphur are liberated from the nitrates and sulphates, with decomposition of the acid radicals; while of the phosphates, the acid group is utilised in the formation of nuclein in the cell nucleus. Iron, which is an essential for all plants, appears to enter into the composition of the nuclein. Calcium salts, although they take no direct part in these processes, seem, nevertheless, to be indispensable. Their importance, indeed absolute necessity, for most plants, is due to their functioning as a medium for conveying the mineral acids, and for neutralising, or precipitating, injurious by-products which are produced in the formation of albumen. The most frequent of these by-products is oxalic acid ($C_2H_2O_4$), which, either as a free acid or as a soluble potassium salt, acts as a poison upon most plants. The oxalate of potassium, which is first formed from the potassium nitrate, reacts with the calcium salts present, with the formation of calcium oxalate, which is only slightly soluble, and, as it accumulates, crystallises out and thus becomes harmless. Wherever the formation of albumen or nuclein takes place, oxalic acid is formed, the calcium salts of which may usually be found in adjacent cells often in enormous quantities, in the form of aggregates of crystals, raphides, or crystal sand.

On account of their occurrence and behaviour in plants, the amides and hexa-carbon bases are regarded as preliminary stages in the formation of albuminous substances. Among the amides asparagin, $C_2H_3(NH_2)(CONH_2)(COOH)$, is noteworthy on account of its wide distribution. It is present in abundance in *Gramineae* and *Leguminosae* (one litre of sap from Bean seedlings contains about 12-15 grammes). In the *Cruciferae* and *Cucurbitaceae* it is replaced by glutamin, while in the *Coniferae* a hexa-carbon base (arginin, $C_6H_{14}N_4O_2$) appears to play the same rôle. Any real knowledge of the mode of origin and transformation into more complicated albuminous compounds of these and similar nitrogenous substances (*e.g.* betain, leucin, tyrosin, and allantoin) is at present wanting.

The colloidal nature of many albuminous substances, which hinders their osmotic diffusion, is of importance since it facilitates their recognition by appropriate reactions and their localisation in the protoplasm ([36 a]).

Transfer of the Products of Assimilation

When colloidal proteid substances are to be conveyed through the tissues, as, for example, from seeds rich in proteids into the seedlings, they are first decomposed into soluble substances. According to SCHULZE ([36 b]), albumoses and peptone are first formed, and these are then broken up into amides and hexa-carbon bases (*e.g.* arginin), and sometimes even into compounds of ammonia. They are in this diffusible form transferred to places where, in combination with carbohydrates and mineral acids, they are used anew in the formation of albumen.

In addition to the transfer of nitrogenous constructive material through the parenchymatous tissues, the LONG-DISTANCE TRANSPORT OF THE READY-FORMED ALBUMINOUS SUBSTANCES seems rather to take place through the open sieve-tubes of the bast. It appears to be in the sieve-tubes, which contain, during life, albuminous substances, starch grains, drops of oil, and leptomin (p. 77), that the conduction of organic substances is effected from the leaves to the roots. In fact, it was long ago concluded that the increased thickening of the cortical layers observed just above wounds made by ringing trees, was due to the interruption and detention of a flow of nourishing sap through the bast towards the roots.

The transfer of the carbohydrates through unbroken cell walls to the various points of consumption can only be accomplished when they are in solution. In case they are not already dissolved in the cell sap, in the form of glucose, maltose, sugar, or inulin, they must first be converted into soluble substances. This is of the highest importance for the transfer and utilisation of starch and reserve cellulose. The former is converted by the influence of DIASTASE into glucose or maltose.

Diastase belongs to those peculiarly acting substances termed UNORGANISED FERMENTS OR ENZYMES, which possess the remarkable power of decomposing or transforming certain organic compounds without themselves becoming changed or consumed in the process. By virtue of this property they are enabled to transform unlimited quantities of certain substances. According to their most important physiological properties, diastatic, peptonising or proteolytic, and inverting enzymes are recognised, which act on starch, albuminous substances, and sugars respectively. These groups do not, however, exhaust the various ways in which these substances, which play such an important part in the chemical changes taking place in the organism, act. Thus there are trypsin-like ferments which dissolve albumen in an alkaline medium, ferments which dissolve membranes of cellulose, wood, or chitin, those that decompose glucosides and oils, and others that convert urea into ammonium carbonate. These and other enzymes have been found in plants, and there is no doubt that such bodies play a part in many imperfectly understood processes, especially in Fungi. A point which the enzymes named above have in common is their hydrolytic mode of action. They introduce the elements of water into the substance acted on, starch ($C_6H_{10}O_5$), for example, being converted into soluble glucose ($C_6H_{12}O_6$).

BUCHNER discovered that the expressed sap of the yeast-plant, even after being filtered, is able to transform grape-sugar into alcohol and carbonic acid. He ascribed this property to a special enzyme termed zymase. This substance, which approximates to the oxydases (*i.e.* enzymes which act by introducing oxygen), differs so widely in some of its properties from the known enzymes that it is a question whether it is really of the same nature.

Enzymes are for the most part colloidal albuminous substances which are formed from the protoplasm, and exhibit a so-called catalytic mode of action. They are easily rendered inactive by poisons or by too high a temperature. Inorganic substances, such as finely-divided iridium or platinum, exhibit a similar catalytic action to enzymes. Their power of exciting fermentation is thus not due to any vital property; they are simply chemical substances, and like them, when in solution, may be precipitated, etc., without losing any of their active principles. Diastase, for example, may be extracted from germinating barley seeds by water or glycerine. After it has been precipitated by means of alcohol and dried to a powder, it may again be dissolved in water, and will still be in a condition to transform enormous quantities of starch, especially if in the form of paste, into sugar (36 c).

Other substances similar to diastase, and also capable of dissolving starch, are widely distributed throughout the vegetable kingdom, and are classed together as diastatic ferments. They are especially abundant in starchy germinating seeds, as well as in tubers and bulbs, in leaves and young shoots. They have also been found, strange to say, in organs where there was no starch for them to act upon. The diastatic transformation and dissolution of the starch is accomplished in a peculiar manner. The starch grain is not dissolved as a homogeneous crystal, uniformly from the surface inwards, but becomes corroded by narrow canals, until it is finally completely disorganised and falls into small pieces (Fig. 185).

The transformation of the starch formed in the chlorophyll corpuscles during the day, takes place, as a rule, at night; for in the daytime the action of the diastatic ferment is counterbalanced by the formation of new starch. The glucose which is thus produced in the leaves passes out of the mesophyll cells into the elongated cells of the vascular bundle-sheaths. The glucose and maltose are transferred in these CONDUCTING SHEATHS through the leaf-stalks into the stem. Thence they are conveyed to the young shoots and buds or carried down to the roots; in short, they are finally transported to places where they are required for the nutrition of the plant. The glucose and maltose often become converted into other carbohydrates during their passage

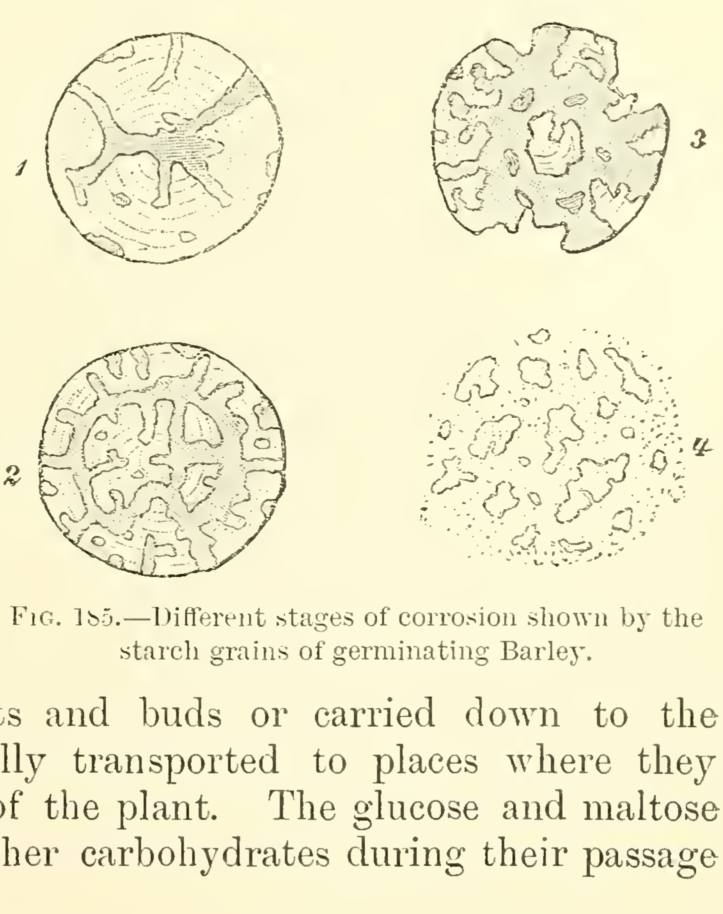


FIG. 185.—Different stages of corrosion shown by the starch grains of germinating Barley.

from one organ to another, particularly into starch. Starch thus formed from other carbohydrates, and not directly by assimilation, is often referred to as TRANSITORY STARCH, and is usually distinguishable by the smaller size of the grains. At the points of consumption these carbohydrates are again converted into glucose, in which condition alone they seem adapted for direct nutrition.

The Storage of Reserve Material

All the products of assimilation are not at once consumed. In spite of this, however, assimilation is continued, and the surplus products beyond the requirements of immediate consumption are accumulated as RESERVE MATERIAL for future use. In our herbs, bushes, and trees, as the yearly growth and consequent consumption cease at the end of each vegetative period, and as the assimilating organs have by that time attained their greatest expansion and efficiency, the surplus of reserve material is the greatest at the close of the season, and is stored in special RESERVOIRS OF RESERVE MATERIAL. All growth of the succeeding year, either of the plants themselves or of their embryonic offspring, is dependent upon the existence somewhere of a supply of reserve material, which may be utilised by the plant until the organs of assimilation are developed. Reserve materials will accordingly be found stored in different forms in the cells of the embryo, or in the surrounding tissues of the seed, in underground rhizomes, tubers, bulbs, and roots, or in the cortical layers, the medullary rays, the wood parenchyma (especially the fibres), and the medulla of persistent stems. Conveyed to these depositories of reserve material, the glucose and maltose are again converted into other carbohydrates, usually starch, which is formed from them by the activity of the starch-producing leucoplasts. In other cases the reserve carbohydrates take the form of cane-sugar (the sugar-beet contains 5-8 per cent, and selected varieties 18 per cent), inulin, or reserve cellulose (*e.g.* vegetable ivory in the fruit of *Phytelephas*). Still more remarkable is the transformation of carbohydrates into fats and oils, occurring in the ripe and ripening seeds of many plants, in fruits (Olive), and also in strictly vegetative tissues. In winter the starch in the wood of many trees also becomes converted into oil, but in the succeeding spring it is again changed to starch. It is finally, at the opening of the buds, converted into glucose or maltose, and conveyed by the transpiration current to the young shoots. Other receptacles of reserve material contain scarcely any carbohydrate, but on the other hand there is much more albuminous matter in the form of thick protoplasm, aleurone grains, protein crystals, and fats (seeds of *Ricinus*). That in the germination of young plants similar tissues with protoplasm, nucleus, cell walls, etc., are formed from these different materials, seems to indicate that all these constructive materials are of almost equal value to the plants. This is due to the fact that plants can, apparently without difficulty, transform the carbohydrates, fats, or albuminous substances one into the other, a result not yet accomplished by chemical processes.

Other Products of Metabolism

The chemical activity of the vegetable cell is by no means exhausted in the production of the substances mentioned: the increasing number of chemical compounds found to be derived from the first product of assimilation is a matter of continual surprise. Of most of them neither the manner of their formation nor their full importance in metabolism is understood. The conditions are not even fully known which are necessary for the formation and functional activity of the ORGANIC ACIDS (malic, tartaric, citric, etc., which may in part be considered as products of imperfect respiration) and TANNINS, although both are so frequent in plants. The function of the GLUCOSIDES is also imperfectly understood. These are nitrogenous and non-nitrogenous compounds, and are not widely distributed. They are soluble in water, and by the action of ferments or dilute acids are broken up into glucose and other derivative products. It is conceivable that a local combination of such diffusible substances plays a part in the formation of glucosides and tannins. In the *Amygdalaceae* they appear as AMYGDALIN, in the *Solanaceae* as the poisonous SOLANIN, in the *Cruciferae* (mustard seeds) as MYRONIC ACID, in the bark of the Horse-chestnut as the extremely fluorescent ÆSCULIN, in species of *Digitalis* as the poisonous DIGITALIN. Certain plants (*Indigofera, Polygonum tinctorium*) contain indican, the glucoside of indoxyl; the latter substance is converted by oxidation into indigo. According to BEYERINCK, Woad (*Isatis tinctoria*) contains free indoxyl ([37]). CONIFERIN, which is contained in lignified cell walls, and especially in the cambial sap of the Conifers, is also included in the glucosides. Coniferin has recently acquired an economic value, as from it VANILLIN, the aromatic principle of vanilla, may be artificially produced. In this process the coniferin is decomposed, through the action of a ferment or acid, into glucose and coniferylalcohol, through the oxidation of which its aldehyde, vanillin, is formed. (According to BUSSE, this substance is contained in the leaves of the *Vanilla* plant in combination with a glucoside, and becomes free from the latter as the fruit ripens.)

It is as yet unknown what part in the metabolic processes of plants is performed by the BITTER PRINCIPLES, such as the LUPULIN of Hops, ALOIN of Aloes, ABSYNTHIN of Wormwood. There is the same uncertainty with regard to the functions of the ALKALOIDS. Since most alkaloids, STRYCHNIN, BRUCIN, VERATRIN, CONIIN, MUSCARIN, ATROPIN, QUININ, MORPHIN, CODEIN, COFFEÏN (theïn), THEOBROMIN, ACONITIN, COLCHICIN, NICOTIN, PILOCARPIN, COCAINE, etc., are violent poisons, their vegetable bases and repugnant bitter principles furnish a certain protection to plants against destructive animals. This, however, does not preclude the possibility that they, like the poisonous oxalic acids, may at the same time have an important physiological significance. Thus, according to TREUB, hydrocyanic acid plays the same part in the formation and transport of proteids in *Pangium edule* as the amides do in other plants ([38]).

The COLOURING MATTERS and ETHEREAL OILS, although in actual weight present only in small quantities, make themselves particularly noticeable to the senses of sight and smell. They probably represent only by- and end-products of metabolism; and, with the exception of chlorophyll, take no further part in the vital processes of plants, except in so far as they are beneficial to the general well-being by enticing (*e.g.* flowers, fruits) or repelling animals. Their œcological significance is accordingly much better known than their physiological function. Just as the ethereal oils are frequently found in special excretory receptacles, the RESINS, GUM-RESINS, and GUM-MUCILAGES, which are also excretion products, are usually deposited in canals or glandular cavities, and are often mixed with ethereal oils. Whether their formation in the particular instances is necessary for the carrying out of the normal processes of metabolism is altogether uncertain. They are, at any rate, useful to plants when wounded, serving as a protection against evaporation and the attacks of parasites. On a square centimetre of the surface of the splint-wood of the Pine, sixty to seventy resin canals open, and the wood contains, according to MAYR, 22 kilos. of resin in every cubic metre.

The significance of the so-called india-rubber (CAOUTCHOUC) and GUTTA-PERCHA in the latex in the economy of the plant is still less known. In addition to these substances, there also occur in latex, resins, ethereal oils, alkaloids (in opium), leptomin, starch grains and other carbohydrates, oil-drops and albuminous substances. The presence of these substances, which are valuable as constructive material, and occasionally also of active enzymes (peptonising ferments are found in the milky juice of *Ficus Carica* and *Carica Papaya*), gave rise to the suggestion that the latex cells and tubes function in the transport of the nutrient matter. It has, however, been found that, even in starved plants, the latex remains unconsumed; and the present knowledge of these often caustic and poisonous saps is limited to their external utility in the economy of plant life. By their obnoxious properties they defend plants from the attacks of enemies. Also, in the event of plants being wounded, the latex is pressed out either by the surrounding turgescent tissue or by the tension of the elastic walls of its own cells, and forms, as it quickly coagulates in the air, an efficient covering for the wound. In other plants, especially in trees, wound-gum serves the same purpose.

Special Processes of Nutrition

Parasites, Saprophytes, Symbionts, and Insectivorous Plants.—The acquisition of organic nutritive substances through the activity of assimilating green cells is the most frequent, and is consequently considered the normal method of plant nutrition. Other modes of nutrition are only possible at the cost of organic substances already produced by the assimilating activity of green plants. Some plants forego all attempts to develop an adequate chlorophyll apparatus, and by so doing lose all ability to provide themselves with nourishment from the inorganic matter about them.

Great numbers of such colourless plants derive their nourishment from the bodies of dead animals and plants. All organic matter at one time or another falls into the power of such plants as are devoid of chlorophyll; it is chiefly due to their decomposing activity in the performance of the nutritive processes that the whole surface of the earth is not covered with a thick deposit of the animal and plant remains of the past thousands of years. These peculiar plants are not satisfied with the possession of the lifeless matter alone; they even seize upon living organisms, both animal and vegetable, in their search for food.

It is chiefly the vast number of Fission-Fungi (Bacteria) and true Fungi which nourish themselves in this way as PARASITES (upon living organisms) or as SAPROPHYTES (upon decaying remains of animals and plants). But even some species of the most widely separated families of the higher phanerogamic plants have also adopted this method of obtaining food.

As a result of this modification of their manner of life, the organisation and functions of these higher plants have undergone the most remarkable transformation. From the corresponding changes in their external appearance, it is evident how far-reaching is the influence exercised by the chlorophyll. With the diminution or complete disappearance of the chlorophyll, and consequent adoption of a dependent mode of life, the development of large leaf surfaces, so especially fitted for the work of assimilation, is discontinued. The leaves shrink to insignificant scales, for with the loss of their assimilatory activity the exposure of large surfaces to the light is no longer essential for nutrition. For the same reason active transpiration becomes unnecessary; the xylem portion of the vascular bundle remains weak, and secondary wood is feebly developed. In contrast to these processes of reduction resulting from a cessation of assimilation, there is the newly-developed power in the case of parasites to penetrate other living organisms and to deprive them of their assimilated products. In saprophytic plants, however, where the question is merely one of absorbing nourishment from organic remains, the external adaptations for taking up nourishment continue more like those for absorbing the mineral salts from the soil, for it then depends only upon an intimate union with the decaying substances.

Cuscuta europaea (Fig. 186), a plant belonging to the family of the *Convolvulaceae*, may be cited as an example of a parasitic Phanerogam. Although, through the possession of chlorophyll, it seems to some extent to resemble normally assimilating plants, in reality the amount of chlorophyll present is so small that it will be at once evident that *Cuscuta* (Dodder) affords an example of a well-equipped parasite.

The embryonic *Cuscuta* plantlet, coiled up in the seeds, pushes up from the ground in the Spring, but even then it makes no use of its cotyledons as a source of nourishment; they always remain in an undeveloped condition (Fig. 186, at the right). Nor does any underground root system develop from the young rootlet, which soon dies off. The seedling becomes at once drawn out into a long thin filament, the free end of which moves in broad circles, and so inevitably discovers any plant, available as a host, that may be growing within its reach. In case its search for a host plant is unsuccessful, the seedling is still able to creep a short distance further at the expense of the nourishing matter drawn from the other extremity of the filament, which then dies off (t) as the growing extremity lengthens. If the free end, in the course of its circular movements, comes ultimately into contact with a proper nourishing plant, such as, for example, the stem of a Nettle or a young Willow shoot (Fig. 186, in the centre), it twines closely about it like a climbing plant. Papillose protuberances of the epidermis are developed on that side of the parasitic stem in contact with the host plant, and pierce the tissue of the host. If the conditions are favourable, these PRE-HAUSTORIA are soon followed by special organs of absorption, the HAUSTORIA (*H*). These arise from the internal tissues of the parasite, and possess, in a marked degree, the capability of penetrating to a considerable depth into the body of the host plant by means of solvent ferments and the pressure resulting from their own growth. They invade the tissues of the host, apparently without difficulty, and fasten themselves closely upon its vascular bundles, while single hypha-like filaments produced from the main part of the haustoria penetrate the soft parenchymatous cells and absorb nourishment from them. A direct connection is formed between the xylem and phloem portions of the bundles of the host plant and the conducting system of the parasite, for in the thin-walled tissue of the haustoria there now develop both wood and sieve-tube elements, which connect the corresponding elements of the host with those of the parasitic stem (Fig. 186, at the left).

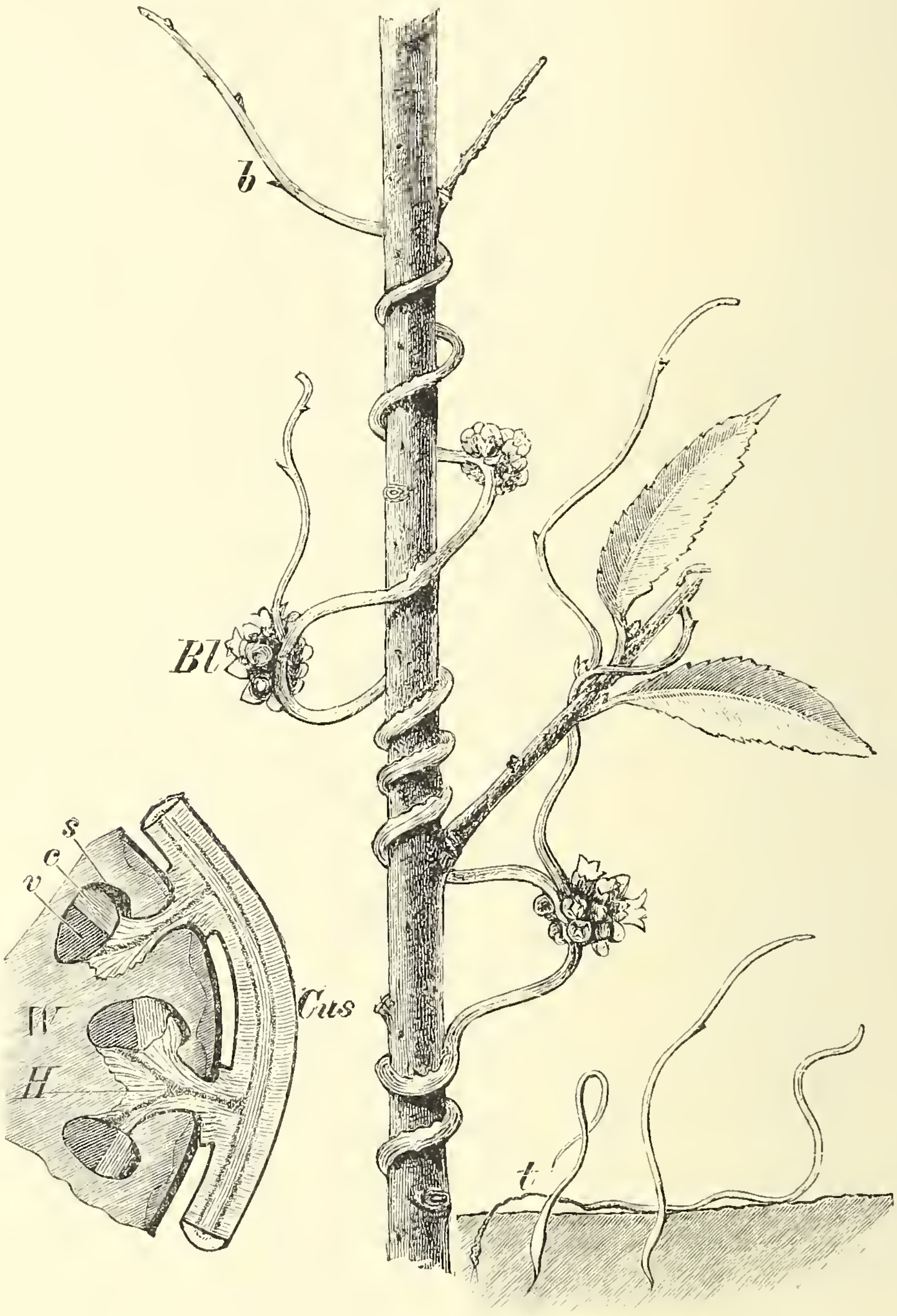


FIG. 186.—*Cuscuta europaea.* On the right, germinating seedlings. In the middle, a plant of *Cuscuta* parasitic on a Willow twig; *b*, reduced leaves; *Bl*, flower-clusters. On the left, cross-section of the host plant *W*, showing haustoria *H* of the parasite *Cus*, penetrating the cortical parenchyma and in intimate contact with the xylem *v* and the phloem *c* of the vascular bundles; *s*, ruptured cap of sheathing sclerenchyma.

Like an actual lateral organ of the host plant, the parasite draws its transpiration water from the xylem, and its plastic nutrient matter from the phloem of its host.

The haustoria of *Orobanche* (Broom rape), another parasite, penetrate only the roots of the host plant, and only its light yellow or reddish-brown or amethyst-coloured flower-shoot appears above the surface of the ground. *Orobanche*, like *Cuscuta*, also contains a small amount of chlorophyll. Both are dreaded pests; they inflict serious damage upon cultivated plants, and are difficult to exterminate.

Many parasitic plants, especially the *Rafflesiaceae*, have become so completely transformed by their parasitic mode of life that they develop no apparent vegetative body at all; but grow altogether within their host plant, whence they send out at intervals their extraordinary flowers. In the case of *Pilostyles*, a parasite which lives on some Asiatic species of *Astragalus*, the whole vegetative body is broken up into single cell filaments, which penetrate the host plant like the mycelium of a fungus. The flowers alone become visible and protrude from the leaf-axils of the host plant (^{39}).

In addition to these parasites, which have come to be absolutely dependent upon other plants for their nourishment, there are certain parasites which, to judge by external appearances, seem to be quite independent, for they possess large green leaves with which they are able to assimilate vigorously. In spite of this, however, these plants only develop normally, when their root system is in connection with the roots of other plants by means of disc-shaped haustoria. *Thesium*, belonging to the *Santalaceae*, and the following genera of the *Rhinanthaceae*, *Rhinanthus*, *Euphrasia*, and *Pedicularis*, may be mentioned as examples of plants showing these peculiar conditions. The Mistletoe (*Viscum album*), although strictly parasitic, possesses, nevertheless, like many of the allied foreign genera of the *Loranthaceae*, fairly large leaves well supplied with chlorophyll, and fully able to provide all the carbohydrates required. It obtains, however, from the host plant (as HEINRICHER has also shown to be probable in the case of the *Rhinanthaceae*) its supply of water and dissolved salts. Another member of the *Rhinanthaceae*, *Melampyrum*, has, on the other hand, adopted a saprophytic mode of life (^{40}).

Humus plants, like some of the *Orchidaceae* (*Neottia*, *Coralliorrhiza*, etc.), and the *Monotropeae*, are restricted to a purely saprophytic mode of nutrition, and to that end utilise the leaf-mould accumulated under trees.

The roots and rhizomes of these saprophytes stand in most intimate relation with fungal hyphæ. The same indeed holds for the majority of green plants which grow in woods and heaths, where the soil is rich in humus. The fungal hyphæ are sometimes present in coiled masses within the cells of a definite zone of the cortex, only occasional filaments passing outwards to the soil. In other cases the fungus surrounds the young roots with a dense investment of interwoven hyphæ. The former arrangement is spoken of as endotrophic, the latter as exotrophic mycorhiza; the two types are, however, connected by intermediate forms. A direct exchange of substance between the soil and the root would appear impossible in the case of the exotrophic mycorhiza. On this ground, and because, despite the reduced surface exposed to the humus-containing soil by the roots or rhizomes of total saprophytes, these obtain sufficient nutriment, a co-operation of the fungus in the nutrition of such plants has been assumed. The results of culture experiments lend further support to this view. Little is known as to the nature of the relation between the fungus and the saprophyte, however. JANSE and others assume that the presence of the fungus makes combined nitrogen available to the plant, while STAHL (41) sees its use in a better supply of salts from the soil. The latter view, however, could only be a sufficient explanation in the case of green plants.

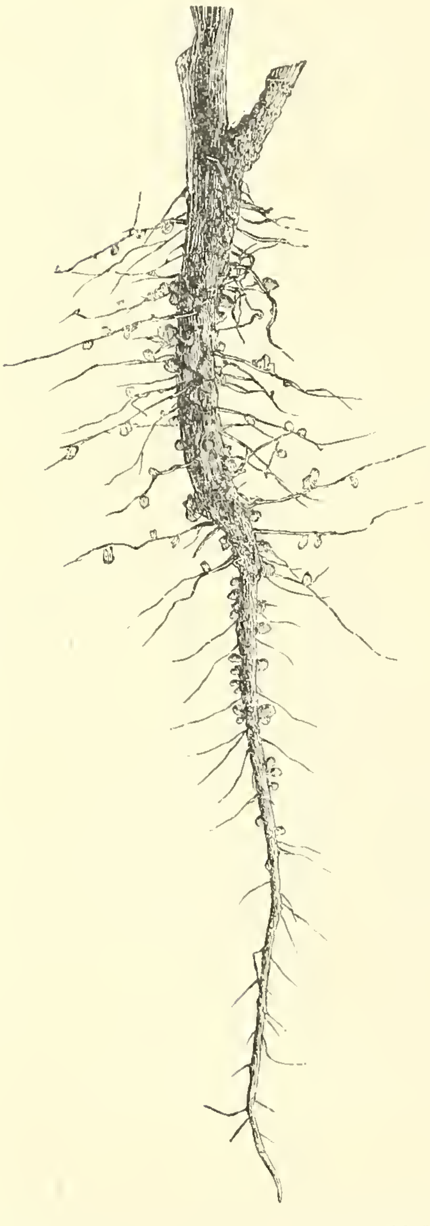


FIG. 187.—A root of *Vicia Faba*, with numerous root-tubercles. (Reduced.)

The relation between roots and Bacteria in the case of the *Leguminosae* is better understood. It has long been known that peculiar outgrowths, the so-called ROOT-TUBERCLES, are found on the roots of many *Leguminosae* (Bean, Pea, Lupine, Clover, etc.) (Fig. 187). Within the last few years, the astonishing discovery has been made that these tubercles, of which a single bean plant may bear 4000, are caused by certain Bacteria, chiefly by *Bacillus radicicola* (*Rhizobium leguminosarum*). These Bacteria penetrate through the root-hairs into the cortex of the roots, and there give rise to the tubercular growths. These tubercles become filled with a bacterial mass, consisting principally of swollen and abnormally developed (hypertrophied) BACTERIOIDS, but in part also of Bacteria, which have remained in their normal condition. The former seem to be eventually consumed by the host plant, while the latter remain with the dead roots in the soil, to provide for future reproduction. As the experiments of HELLRIEGEL and the investigations of NOBBE, BEYERINCK, HILTNER, and others (42) prove, we have here a case of mutual parasitism like those termed symbiosis by DE BARY. While the Bacterium lives on carbohydrates supplied by the host plant, the latter profits by the power of fixing free nitrogen possessed by the Bacteria. While these remain alive they furnish a steady supply of nitrogenous substance to the leguminous plant, and ultimately the remaining substance of the degenerated Bacterioids is absorbed. The fact that the tubercle-forming *Leguminosae* could flourish on ground poor in nitrogen and could accumulate stores of reserve proteids was known in the time of Pliny, and these plants have long been known to form crops which enrich the soil by this accumulation of nitrogen.

If the soil in which such a leguminous plant grows contains a sufficiency of nitrates, few tubercles are formed on the roots. A similar immunity against infection is obtained by plants which bear a number of actively functional tubercles. In addition to the *Leguminosae* (in which order only *Gleditschia triacanthos* has as yet been found free from tubercles) tubercle formation due to a symbiosis with a lower organism is known in *Elaeagnus* and *Alnus*. According to NOBBE and HILTNER, these plants can also utilise free nitrogen. These authors have also shown that the same holds for *Podocarpus*, which possesses mycorhiza, thus giving experimental confirmation to a suggestion of JANSE.

While among the higher plants only isolated forms have become total parasites or saprophytes, while in others the parasitism or saprophytism is occasional or partial, among the lower plants large families with innumerable genera and species are found completely devoid of chlorophyll (Fungi and Bacteria), and altogether parasitic or saprophytic in their mode of life. Of the Fungi and Bacteria some are true parasites, and are often restricted to certain special plants or animals, or even to distinct organs; others, again, are strictly saprophytic in their habit, while others may be either parasitic or saprophytic, according to circumstances. What renders the conduct of these lower organisms particularly striking is the peculiarity possessed by many of them of not fully utilising all of the organic matter at their disposal; but, on the contrary, so decomposing and disorganising the greater part of it by their fermentative activity that their own development soon becomes restricted. When Mucor-fungi attack an apple, they not only take the small amount of organic matter necessary for their sustenance, but at the same time convert the whole apple into a soft decaying mass. In addition to this peculiar nutritive activity, intramolecular respiration (p. 218) is also active in the promotion of fermentation and putrefaction. A considerable degree of heat is also evolved in the course of these processes. The utilisation of this heat in making hot-beds is a familiar practice. The heat produced by damp fermenting hay or raw cotton may often become so great that spontaneous combustion ensues. In germinating Barley an increase in temperature of from 40 to 70 or more degrees has been observed. The development of so much heat in this case is not due solely to the respiration of the barley seeds, but according to COHN, to the decomposing activity of a fungus (*Aspergillus fumigatus*). The spontaneous combustion of raw cotton is, on the other hand, caused by a *Micrococcus*. Coagulated albumen and thick gelatine are rendered fluid by many Fungi and Bacteria, while the escaping gases (carbonic acid, sulphuretted hydrogen, ammonium sulphide, ammonia, etc.) show how deep-seated is the decomposition. In the same way *Penicillium brevicaule* and other Fungi can liberate poisonous arsenical gases when living on a substratum containing arsenic (43). It is by similar processes of decomposition that dead organic matter becomes thoroughly disorganised and rendered harmless. To the toxic substances produced by Fungi and Bacteria is due the severity of many diseases which they produce in living organisms (potato disease, wheat smut, cholera, typhus, diphtheria, anthrax, etc.). By the possession or formation of substances, which react as specific poisons upon the infecting Bacteria, plants, and particularly animals, in turn protect themselves against the attacks of such micro-organisms. It is due to a knowledge of this fact that the science of Therapeutics has been enabled to cope more and more successfully with infectious diseases.

While hitherto micro-organisms have been regarded as the cause of all infective diseases, BEYERINCK has recently discovered a "contagium fluidum" which is unorganised but capable of increase in the plasma of the Tobacco plant (44); it gives rise to the spot disease on the leaves of this plant.

Fungi and Bacteria, in addition to the power, dangerous to themselves, of disorganising their own nutrient substratum by fermentation and putrefaction, also possess the capability of making an unsuitable substratum suitable for their sustenance. By means of inverting ferments they can convert an unsuitable cane-sugar into an available grape-sugar, and by their diastatic ferments they are able to form glucose and maltose from starch, and even from cellulose.

As is evident from their thriving upon such various substrata, Fungi have the power of producing from the most different carbon compounds (and also from nitrogenous mineral compounds such as ammonium tartrate, or even ammonium carbonate) protoplasm, cell wall, nuclein, fat, glycogen, etc.

While many Fungi inflict far greater injury upon their host plants by the decomposition they induce than by the withdrawal of the nutritive substances, others produce a different effect. The Rust-fungi, for instance, do comparatively little injury to their host; while the relation between host and Fungus in the case of the Lichens has been shown to be absolutely beneficial. The Lichens were formerly considered to be a third group of the lower Cryptogams and of equal value with the Algæ and Fungi. It is only in recent years that the discovery was made by DE BARY and verified by the investigations particularly of SCHWENDENER and STAHL, that the body of the Lichens is not a single organism, but in reality consists of Algæ (*e.g.* fission-Algæ), which also exist in a free state, and of Fungi, which for the most part belong to the *Ascomycetes.* The Fungus hyphæ within the Lichen weave themselves around the Algæ; and while the latter occupy the upper or outer side of the leaf-like or cylindrical thallus as the more favourable position for assimilation, the hyphæ come into the closest contact with them and absorb from them part of their assimilated products. The Fungi in return provide the Algæ with nutrient water, and enable them to live in situations in which they could not otherwise exist. The researches of ARTARIS make it probable that peptone is also provided by the Fungus. As a result of this close union with the Fungi, the Algæ are in no way exhausted, but become more vigorous than in their free condition, and reproduce themselves by cell division. As both symbionts, the Algæ as well as the Fungi, thus derive mutual advantage from their consortism, Lichens form one of the most typical examples of vegetable symbiosis (45).

The cause of the regular appearance of the fission-Algæ *Nostoc* and *Anabaena* in the roots of the *Cycadeae* and in the leaves of *Azolla* and other water plants is much less easy to explain (46).

In connection with these cases of symbiosis between plants, mention may here be made of the similar symbiotic relation existing between animals and plants. Like the Lichen-fungi, the lower animals, according to BRANDT, profit by an association with unicellular *Algæ* by appropriating their assimilated products without at the same time disturbing the performance of their functions. Fresh-water Polyps (*Hydra*), Sponges (*Spongilla*), *Ciliata* (*Stentor*, *Paramecium*), also *Heliozoa*, *Planaria*, and *Amoebae* (*A. proteus*) are often characterised by a deep green colour, due to numerous Algæ which they harbour within their bodies, and from the products of whose assimilation they also derive nourishment. In the case of the Radiolarias, the so-called "yellow cells," which have been distinguished as yellow unicellular Seaweeds, function in the same way as the green Algæ in the other instances. Another remarkable example of symbiosis in which the relationship is not one merely of simple nutrition, has been developed between certain plants and ants. The so-called ANT-PLANTS (Myrmecophytes) offer to certain small extremely warlike ants a dwelling in convenient cavities of the stems (*Cecropia*), in hollow thorns (*Acacia spadicigera* and *sphaerocephala*, Fig. 188), in swollen and inflated internodes (*Cordia nodosa*), or in the labyrinthine passages of their large stem-tubers (*Myrmecodia*). At the same time the ants are provided with food in the case of the Cecropias and Acacias in the form of albuminous fatty bodies ("food bodies," Fig. 188, *F*), and by the Acacias also with nectar. The ants in exchange guard the plants most effectively against the inroads of animal foes as well as against other leaf-cutting species of ants, which, in the American tropics, kill trees by completely

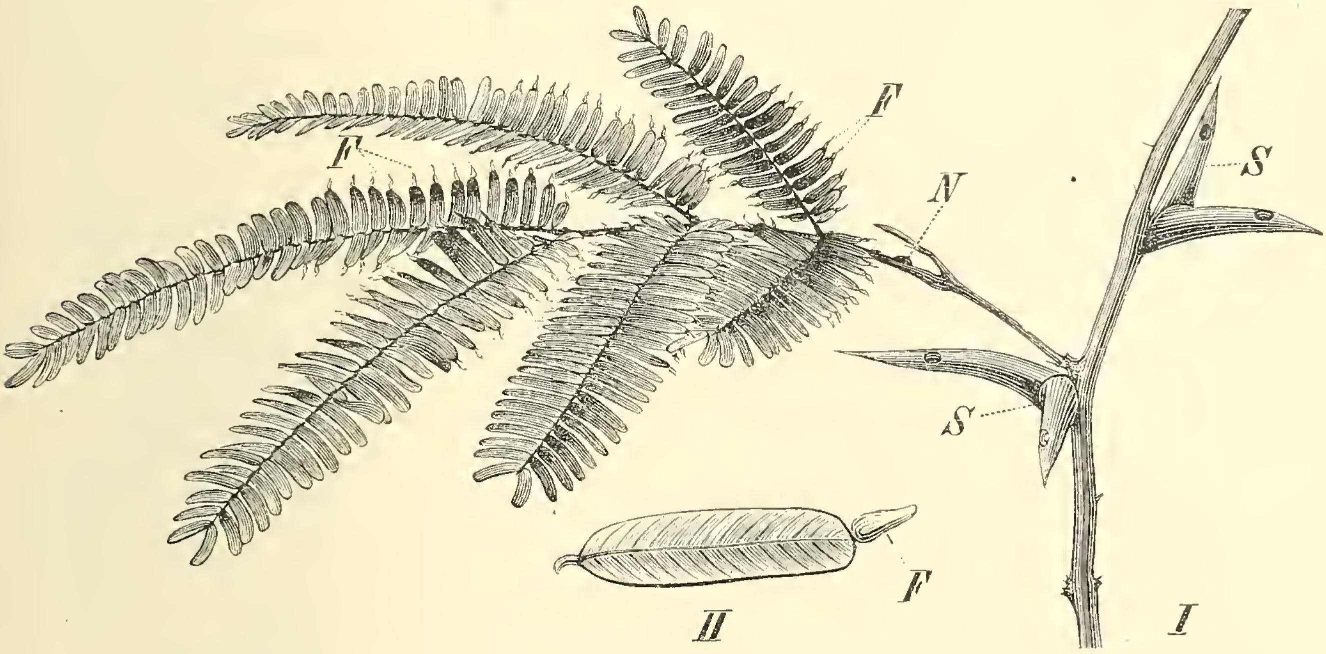


FIG. 188.—*Acacia sphaerocephala*. *I*, Leaf and part of stem; *S*, hollow thorns in which the ants live; *F*, food-bodies at the apices of the lower pinnules; *N*, nectary on the petiole. (Reduced.) *II*, Single pinnule with food-body, *F*. (Somewhat enlarged.)

and rapidly divesting them of their entire foliage. These same leaf-cutting ants live in symbiosis with a Fungus (*Rozites gongylophora*). Upon the accumulated leaves ("Fungus-gardens"), according to MÖLLER, the ants make pure cultures of the fungus mycelium, whose peculiar nutritive outgrowths serve them exclusively for nourishment. Termites have more recently been discovered to be Fungus cultivators (^{47}). Other familiar examples of symbiosis are those existing between flowers and birds or insects. The flowers in these instances provide the nourishment, usually nectar or pollen, but sometimes also the ovules (Yucca-moth and the gall-wasp of the Fig.), while the animals are instrumental in the pollination. Here also each symbiont is dependent upon the other. In the case of the unintentional dissemination of fruits and seeds by the agency of animals, the symbiotic relations are less close.

Of all the different processes of supplementary nutrition employed by plants, those exhibited by Insectivorous Plants in the capture and digestion of animals are unquestionably the most curious. Although they are green plants and in positions to provide their own organic nourishment, they have, in addition, secured for themselves, by peculiar contrivances, an extraordinary source of nitrogenous organic matter, by means of which they are enabled to sustain a more vigorous growth, and especially to support a greater reproductive activity, than would otherwise be possible without animal nourishment.

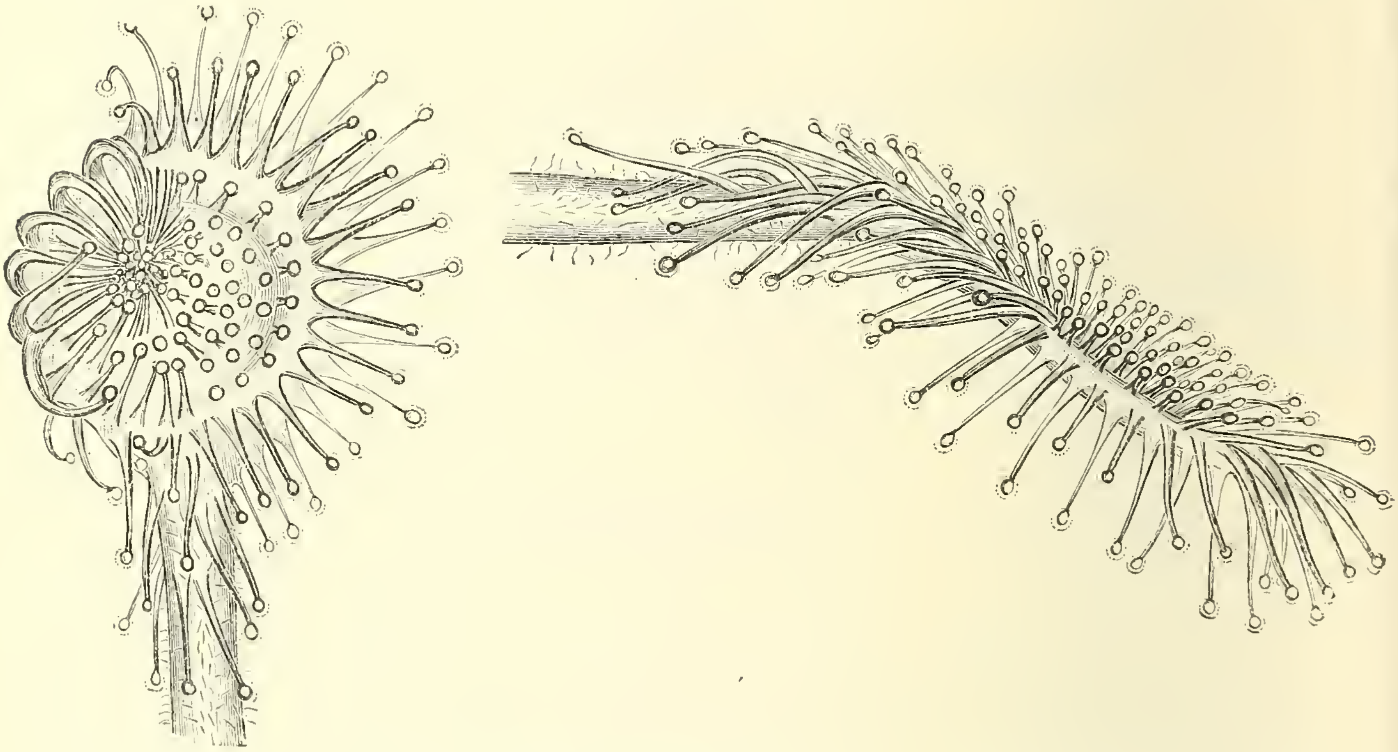


FIG. 189.—Leaves of *Drosera rotundifolia*. That on the left is viewed from above, that on the right from the side. (After DARWIN, enlarged.)

It is not accidental that the plants which have become carnivorous are, for the most part, either inhabitants of damp places, of water swamps, and moist tropical woods, or that they are epiphytes. The nitrogenous and phosphoric salts of the soil are not obtained by them in the same quantities as in the case of the more vigorously transpiring land plants. This is very evidently the case in the Sundew (*Drosera*), which is loosely attached by a few roots upon a thick spongy carpet of

Bog-moss, and must find in the animal food a valuable addition to its nitrogenous nourishment.

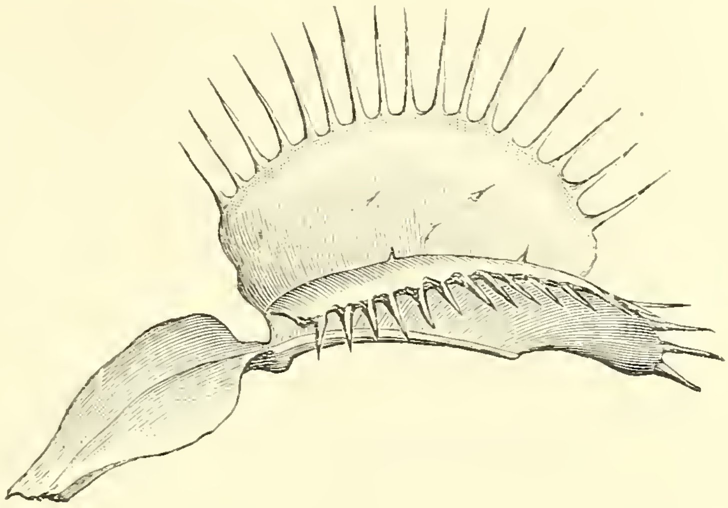


FIG. 190.—A leaf of *Dionaea muscipula*, showing the sensitive bristles on its upper surface, which, in the parts shaded, is also thickly beset with digestive glands. (After DARWIN, enlarged.)

A great variety of contrivances for the capture of insects are made use of by carnivorous plants. The leaves of *Drosera* are covered with stalk-like outgrowths ("tentacles"), the glandular extremities of which discharge a viscid acid secretion (Figs. 189 and 119). Any small insect, or even larger fly or moth, which comes in contact with any of the tentacles is caught in the sticky secretion, and in its ineffectual struggle to free itself it only comes in contact with other glands and is even more securely held. Excited by the contact stimulus, all the other tentacles curve over and close upon the captured insect, while the leaf-lamina itself becomes concave and surrounds the small prisoner more closely. The secretion is then discharged more abundantly, and contains, in addition to an increased quantity of acid, a peptonising ferment. The imprisoned insect, becoming thus completely covered with the secretion, perishes. It is then slowly digested, and, together with the secretion itself, is absorbed by the cells of the leaf.

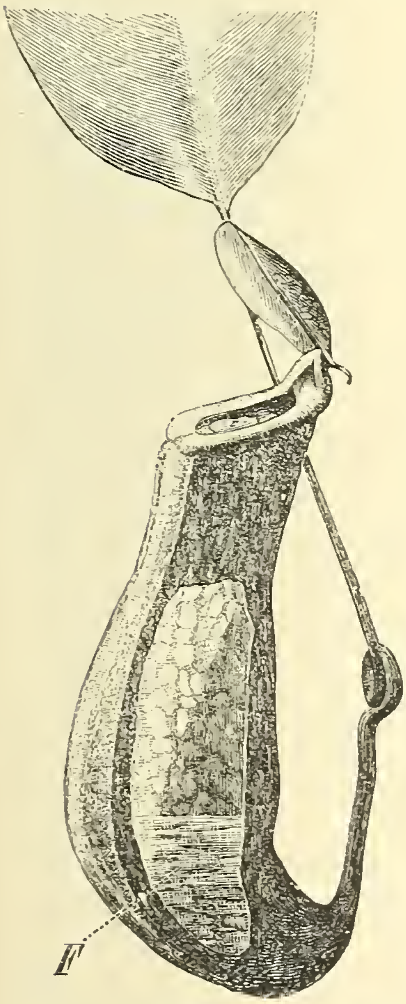


FIG. 191.—Pitchered leaf of a *Nepenthes*. A portion of the lateral wall of the pitcher has been removed in order to show the fluid (*F*), excreted by the leaf-glands. (Reduced.)

In *Pinguicula* it is the leaf-margins which fold over any small insects that may be held by the minute epidermal glands. In species of *Utricularia* (Fig. 46), growing frequently in stagnant water, small green bladders (metamorphosed leaf-tips) are found on the tips of the dissected leaves. In each bladder there is a small opening closed by an elastic valve which only opens inwards. Small snails and crustaceans can readily pass through this opening, guided to it by special outgrowths; but their egress is prevented by the trap-like action of the valve, so that in one bladder as many as ten or twelve crustaceans will often be found imprisoned at the same time. The absorption of the disorganised animal remains seems to be performed by forked hairs which spring from the walls of the bladder.

More remarkable still, and even better adapted for its purpose, is the mechanism exhibited by some exotic insectivorous plants. In the case of Venus Fly-trap (*Dionaea*), growing in the peat bogs of North Carolina, the capture of insects is effected by the sudden closing together of the two halves of the leaves (Fig. 190). This action is especially due to the irritability of three bristles on the upper side of each half-leaf (the leaf surfaces themselves are much less sensitive). Upon the death of the insect caught by the leaf, a copious excretion of digestive sap takes place from glandular hairs on the leaf surface, followed by the absorption of the products of the digestive solution. In the case of other well-known insectivorous plants (*Nepenthes*, *Cephalotus*, *Sarracenia*, *Darlingtonia*), the traps for the capture of animal food are formed by the leaves which grow in the shape of pitchers (Figs. 45, 191). These trap-like receptacles are partially filled with a watery fluid excreted from glands on their inner surfaces. Enticed by secretions of honey to the rim of the pitcher (in the case of *Nepenthes*), and then slipping on the extraordinarily smooth surface below the margin, or guided by the downward-directed hairs, insects and other small animals finally fall into the fluid and are there digested by the action of ferments and acids. In *Sarracenia* and *Cephalotus*, GOEBEL was unable to discover any digestive ferments; but in *Cephalotus*, however, it was possible to determine that the secretions have antiseptic properties. The lid-like appendage at the opening of the pitcher of *Nepenthes*, *Sarracenia*, and *Cephalotus* does not shut; its function seems to be merely to prevent foreign substances from falling into the pitcher, and particularly to keep out the rain. The entrance to the tubular leaves of *Darlingtonia* is under the helmet-like extremity, and therefore a lid is unnecessary.

III. Respiration

It is a matter of common knowledge that animals are unable to exist without breathing. In the higher animals the process of respiration is so evident as not easily to escape notice, but the fact that plants breathe is not at once so apparent. Just as the method of the nutrition of green plants was only discovered by experiment, so it also required carefully conducted experimental investigation to demonstrate that PLANTS ALSO MUST BREATHE IN ORDER TO LIVE; that, like animals, they take up oxygen and give off carbonic acid. Although the question had already been thoroughly investigated by SAUSSURE in 1822, and by DUTROCHET in 1837, and its essential features correctly interpreted, LIEBIG pronounced the belief in the respiration of plants to be opposed to all facts, on the ground that it was positively proved that plants on the contrary decomposed carbonic acid and gave off the oxygen. He asserted that it was an absurdity to suppose that both processes were carried on at the same time; and yet that is what occurs.

ASSIMILATION AND RESPIRATION ARE TWO DISTINCT VITAL PROCESSES CARRIED ON INDEPENDENTLY BY PLANTS. WHILE IN THE PROCESS OF ASSIMILATION **green** PLANTS ALONE, AND ONLY IN THE LIGHT, DECOMPOSE CARBONIC ACID AND GIVE OFF OXYGEN, **all** PLANT ORGANS WITHOUT EXCEPTION BOTH BY DAY AND BY NIGHT TAKE UP OXYGEN AND GIVE OFF CARBONIC ACID. Organic substance, obtained by assimilation, is in turn lost by respiration. A seedling grown in the dark so that assimilation is impossible, loses by respiration a considerable part of its organic substance, and its dry weight is considerably diminished. It has been found that during the germination of a grain of Indian Corn, a full half of the organic reserve material is consumed in three weeks. That green plants growing in the light accumulate a considerable surplus of organic substance, is due to the fact that the daily production of material by the assimilatory activity of the green portions is greater than the constant loss which is caused by the respiration of all the organs. Thus, according to BOUSSINGAULT'S estimates, in the course of one hour's assimilation a plant of Sweet Bay will produce material sufficient to cover thirty hours' respiration. Plants produce in twenty-four hours about five to ten times their own volume of carbonic acid. In shade-plants, according to GRIFFON (48), this is usually reduced to twice the plant's volume, while the commonly cultivated *Aspidistra* produces only one-half its own volume, and can therefore succeed even under conditions which are unfavourable to assimilation.

A means of judging of the importance of respiration is afforded by the behaviour of the plants themselves when deprived of oxygen. By placing them, for example, under a jar containing either pure nitrogen or hydrogen, or in one from which the air has been exhausted, it will then be found that all vital activity soon comes to a stand-still; plants, previously growing vigorously, cease their growth; the streaming motion of the protoplasm in the cells is suspended, as well as all external movement of the organs. If oxygen be admitted, after not too long an interval, the interrupted performance of the vital functions is again renewed. A longer detention in an atmosphere devoid of oxygen will, however, irrevocably destroy all traces of vitality; as in every condition of rigor internal chemical changes take place, which, by a prolonged exclusion of oxygen, lead to the destruction and disorganisation of the living substance. THE PRESENCE OF OXYGEN IS NECESSARY TO THE CHEMICAL PROCESSES TAKING PLACE WITHIN THE CELL, IN ORDER TO MAINTAIN THE LIVING SUBSTANCE IN A CONDITION OF NORMAL ACTIVITY.

The absorption of oxygen and the evolution of carbonic acid by living plants can be demonstrated both qualitatively and quantitatively by simple experiments. From what has already been said of the contradictory nature of assimilation and respiration, it will be at once apparent that these experiments must be conducted either in the dark or on portions of plants devoid of chlorophyll. The more abundant the protoplasm and the more energetic its vital activity, so much the more vigorous is the respiration. The best results are obtained, therefore, from young portions of plants in an active state of growth. It should also be mentioned that in the following experiments only the carbonic acid and not the whole of the products of the respiratory activity are determined. From theoretical considerations, and also from exact chemical analysis, it has been definitely established that, IN ADDITION TO CARBONIC ACID, WATER IS FORMED FROM THE ORGANIC MATTER BY RESPIRATION.

The absorption of oxygen and the formation of carbonic acid may be clearly shown by the following experiment (Fig. 192). A flask (*B*) filled with young mushrooms or Composite flowers is inverted with its mouth in an open vessel of mercury (*Q*), and a few centimetres of caustic potash solution introduced within its neck. In the same degree as the carbonic acid produced by respiration is absorbed by the caustic potash, the volume of air in the flask will be reduced and the mercury will rise in the neck. After a time, the ascent of the mercury ceases and it remains stationary. If the quantity of air remaining in the flask be estimated, it will be found that it has lost a fifth of its original volume ; this means, however, that the whole of the oxygen (which makes up one-fifth of the atmospheric air) has been absorbed. If caustic potash is not used in this experiment to absorb the exhaled carbonic acid, the mercury remains at its natural level, or, in other words, the volume of air in the flask remains unchanged. From this experiment it is apparent that the volume of oxygen absorbed is equal to the volume of carbonic acid evolved, as expressed by the formula $\frac{CO_2}{O_2} = 1$. This equivalence of volume between the oxygen absorbed and the carbonic acid exhaled exists only in cases where the oxygen is used exclusively for respiration, and not where it is consumed in transforming the contents of the cells, as is observed in the germination of seeds rich in fat, and in the interchange of gases in the case of the succulents. In the germination of seeds rich in fat, the fat is converted into carbohydrates richer in oxygen. The oxygen consumed remains combined in the plant. On the other hand, in the case of the succulents, their peculiar power of effecting oxidation during the night and subsequent deoxidation in the light, modifies the gaseous interchange of respiration. The respiratory coefficient may vary within certain limits, according to the state of nutrition of the plant and the conditions to which it is exposed.

The absorption of oxygen in the respiration of plants can also be shown by the fact that a flame, held in a receptacle in which plants have been kept for a time, is extinguished. If a lighted taper be thrust into a glass cylinder which has been partially filled with flowers or mushrooms, and then tightly covered and allowed to remain for a day, it will be extinguished, as the oxygen of the air in the cylinder will all have been absorbed. The carbonic acid exhaled in respiration can be quantitatively determined from the increase in the weight of the caustic potash by which it has been absorbed, or by conducting the respired carbonic acid gas through baryta water and estimating the precipitate of barium carbonate.

Intramolecular Respiration ([49]).—In the middle of the seventies PFLÜGER made the surprising discovery that frogs are not only able to live for some time in an atmosphere devoid of oxygen, but even continue to exhale carbonic acid. From similar investigations it was found that plants also, when deprived of oxygen, do not die at once, but can prolong their life for a time and evolve carbonic acid. Under these circumstances it is apparent that both elements, the carbon as well as the oxygen, must be derived from the organic substance of the plants themselves : the oxygen can only be obtained through some unusual process of decomposition carried on within the plant. This form of respiration has consequently been described as intramolecular.

The amount of carbonic acid produced in a given time by intramolecular respiration is usually less than that given off in the same time during normal respiration. There are plants, however (for instance, *Vicia Faba*), whose seedlings, in an atmosphere of pure hydrogen, will exhale for hours as much carbonic acid as in the ordinary air. During intramolecular respiration in aerobionts all growth ceases and abnormal processes of decomposition take place, whereby alcohol and other products are formed.

Intramolecular respiration commences as soon as the access of free oxygen to the protoplasm is prevented, and continues until the latter is killed by the accumulation of injurious products of decomposition. The sufficiently early readmittance of oxygen may, however, permit the cell to resume its normal condition by re-establishing ordinary respiration and removing the accumulated decomposition products.

Some plants endure the absence of free oxygen badly and only for a short time, others better and for a longer period. Certain of the lower plants (*Bacteria*, *Fungi*, *Characeae*) can exist for a considerable time without free oxygen, or are even able under favourable conditions to find a complete substitute for the ordinary oxygen-respiration in intramolecular respiration. This capability is so extreme in some *Bacteria* that no trace of free oxygen is necessary for their existence, while some cannot live in the presence of oxygen. To distinguish such specially adapted organisms from those which depend for their normal respiration on free oxygen (aerobionts or aerobes) they are termed anaerobionts or anaerobes. The grades of independence of free oxygen indicated above may be distinguished as temporary or facultative anaerobiosis and permanent or obligate anaerobiosis respectively.

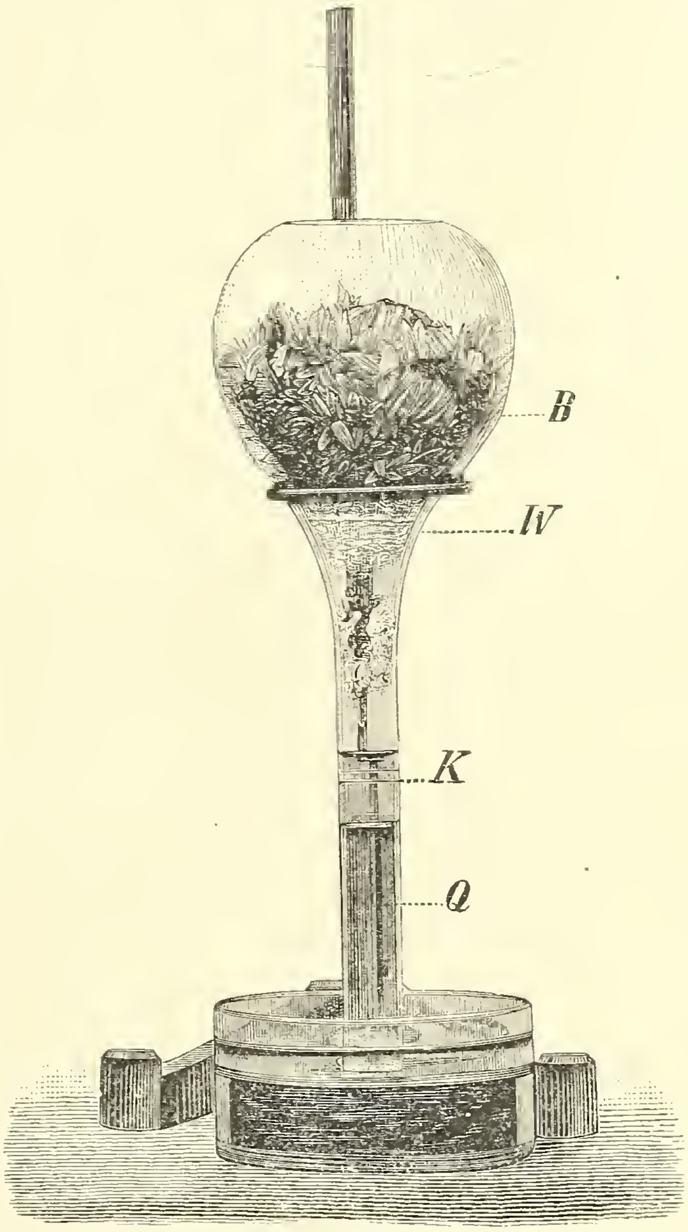


FIG. 192.—Experiment in respiration. The inverted flask (*B*) is partially filled with flowers, which are held in place by the plug of cotton (*W*). Through the absorption of the carbonic acid exhaled in respiration, by the solution of caustic potash (*K*), the mercury (*Q*) rises in the neck of the flask.

Respiration as a Source of Energy.—That the metabolic change constituting respiration is a necessary concomitant of life may be inferred from the cessation of vital manifestations when respiration is interfered with, and the association of more active life with increased demands on the respiratory process.

In respiration chemical changes occur leading to the setting free of energy. It is hardly too much to say that it is the energy obtained by respiration which serves to carry on and maintain the vital manifestations. Thus a specific vital energy is obtained by means of respiration, which might be termed vital force were this term not used in another sense ; such a supply of energy is not provided by other sources of force in the plant (force of pressure in turgescence, vibrations of light and heat rays, etc.).

The majority of plants sacrifice in physiological combustion a portion of their organic substance (especially carbohydrates) in order to obtain this driving power. The combustion is as a rule so complete that CO_2 and H_2O are the resulting products; this not only obtains the maximum of energy but obviates the accumulation of injurious products of respiration. In other cases, however, considerable amounts of organic acids are formed, together with the CO_2 and H_2O. The latter modification, which is found in succulents living under unfavourable conditions for assimilation, avoids the loss of carbon attendant on the liberation of CO_2 into the air.

The energy liberated by the respiratory combustion of carbon-compounds is traceable back to that stored in the form of potential energy of chemical combination in carbohydrates, which were formed by the help of the sun's rays in assimilation (cf. p. 196). Energy is not only liberated in the more or less complete combustion of carbon-compounds but may be obtained in other chemical processes. Thus sulphur-bacteria oxidise sulphuretted hydrogen to sulphur, and this in turn to sulphuric acid. The nitrite-bacteria form nitrous acid from ammonia and amides, while nitrate-bacteria convert the nitrous into nitric acid. The energy obtained in such processes may serve to replace the driving power of respiration, or, as has been shown for the nitro-bacteria (p. 197), may effect the synthesis of organic carbon-compounds. The working power is thus devoted to one or other process of the life of the plant, just as in a manufactory electrical energy may serve to drive machines, afford a source of light, or effect chemical changes (^{50}).

Fermentation and Respiration.—In the section on special modes of nutrition it was stated that when this is effected at the expense of organic food material, fermentation is frequently set up in the substratum. Since fermentation is a process of decomposition associated with a liberation of energy stored in organic compounds, it may be serviceable in the same way as respiration. Its amount may also be more or less influenced by the respiratory needs of the organism.

Thus, when the yeast plant is living as an anaerobe, the greater part of the organic substratum (about 98-99 per cent) is fermented. When growing as an aerobe, with a full supply of oxygen, a larger amount of the substratum is available for use in the processes of growth and multiplication.

Since, even in the latter case, a large part of the grape-sugar (according to BUCHNER and RAPP about 85 per cent) is fermented, it may be concluded that the process of fermentation, though under certain circumstances a source of energy to the plant, is to some extent independent of the respiratory needs of the latter. Oxygen-respiration is also to a certain extent independent of the other vital manifestations. It is most active at a temperature a little below that which causes the death of the organism, when all other activities are being arrested by the heat. The vital processes of the cells, while dependent on the metabolic changes in which energy is set free, resemble the action of a steam engine which may cease even though the furnace is in full blaze. The vital manifestations in the same way need not under all circumstances keep pace with the variations in intensity of the processes which supply the necessary energy.

Heat produced by Respiration.—Respiration is, chemically and physically considered, a process of oxidation or combustion, and, like them, is accompanied by an evolution of heat. That this evolution of heat by plants is not perceptible is due to the fact that considerable quantities of heat are rendered latent by transpiration, so that transpiring plants are usually cooler than their environment; and also to the fact that plants possess very large radiating surfaces in proportion to their mass. The spontaneous evolution of heat is easily shown experimentally, if transpiration and the loss of heat by radiation are prevented and vigorously respiring plants are selected. Germinating seeds (Peas), if examined in large quantities, show under proper conditions a rise in temperature of 2° C. The greatest spontaneous evolution of heat manifested by plants has been observed in the inflorescence of the *Araceae*, in which the temperature was increased by energetic respiration 10°, 15°, and even 20° C. Also in the large flower of the *Victoria regia* temperature variations of 15° C. have been shown to be due to respiration. One gramme of the spadix substance of an Aroid exhales, in one hour, up to 30 cubic centimetres CO_2; and half of the dry substance (the reserved sugar and starch) may be consumed in a few hours as the result of such vigorous respirations. In the process of wound-healing in plants a noticeable rise in temperature also occurs.

That other processes, in addition to respiration, co-operate in the production of heat is apparent from the fact that the amount of heat evolved does not vary proportionally to the carbonic acid exhaled.

The Movement of Gases in Respiration

In plants of simple construction the cells which are in direct contact with the air or water can absorb the requisite oxygen directly; while cells in the midst of tissues are dependent upon the oxygen which can diffuse through the surrounding cells. Such a diffusion from cell to cell would not, however, be adequate, in the case of the vast cellular bodies of the higher plants, to provide the living cells of the interior with a sufficient supply of oxygen. This is accomplished by means of the air-spaces, which, as INTERCELLULAR PASSAGES, penetrate the tissues in all directions and so bring to the protoplasm of the inner cells the air entering through the STOMATA and LENTICELS (p. 141). The path of the respiratory gases is thus the same as that followed by the gases in transpiration and assimilation (pp. 188, 200). It is, however, only the more superficial tissues which are concerned in these latter processes.

The movement of the gases within the intercellular spaces is due partly to the diffusion, induced by the constant interchange of gases caused by respiration, assimilation, and transpiration, and partly to their own instability, arising chiefly from modifications of the temperature, pressure and moisture of the surrounding atmosphere, but which is also increased by the movement of the plants themselves, through the action of the wind.

That the intercellular spaces were in direct communication with each other and also with the outer atmosphere was rendered highly probable from anatomical investigation, and has been positively demonstrated by physiological experiment. It is, in fact, possible to show that air forced by moderate pressure into the intercellular passages makes its escape through the stomata and lenticels; and conversely, air which could enter only through the stomata and lenticels can be drawn out of the intercellular passages. The method of conducting this experiment can be seen from the adjoining figure (Fig. 193).

Intercellular air-spaces are extensively developed in water and marsh plants, and occupy the greater part of the plant body. The submerged portions of water plants unprovided with stomata thus secure a special INTERNAL ATMOSPHERE of their own, with which their cells maintain an active exchange of gases. This internal atmosphere is in turn replenished by the diffusion taking place with the surrounding atmosphere. In marsh plants, which stand partly in the air, the large intercellular spaces form connecting canals through which the atmospheric oxygen, without being completely exhausted, can reach the organs growing deep in the swampy soil, surrounded by marsh-gas and otherwise cut off from any communication with the atmosphere. (On respiratory roots cf. p. 46).

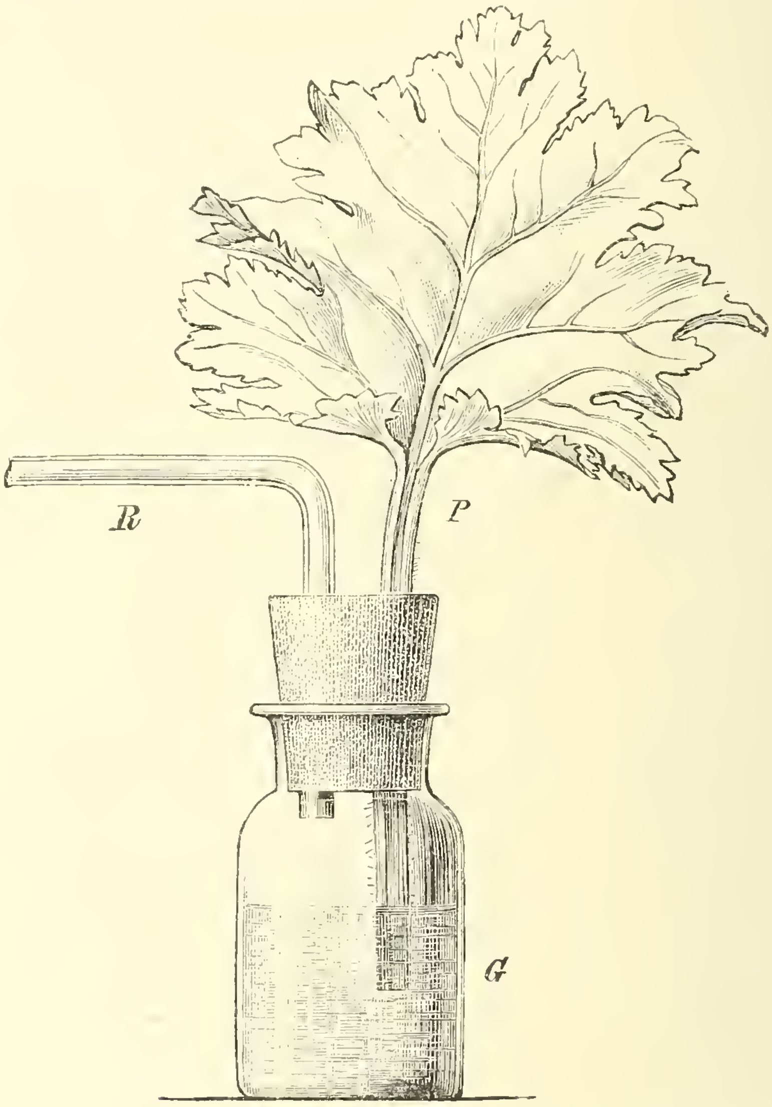


Fig. 193.—Experiment to show the direct communication of the external atmosphere with the internal tissues of plants. The glass tube *R*, and the leaf *P*, are fitted air-tight in the bottle *G*; upon withdrawal of the air in the bottle by suction on the tube *R*, the external air penetrates the intercellular spaces of the leaf, through the stomata, and escapes in the form of small air-bubbles from the cut surface of the leaf-petiole. (From DETMER's *Physiol. Pract.*)

Phosphorescence.—The same conditions which accompany respiration also give rise to the production of light or phosphorescence in a limited number of plants, particularly in Fungi and Bacteria. This phosphorescence at once disappears in an atmosphere devoid of oxygen, only to reappear on the admission of free oxygen. All the circumstances which facilitate respiration intensify phosphorescence; the converse of this is also true. According to the results of investigations concerning the phosphorescence of animals, from which that of plants does not probably differ in principle, the phosphorescence is not directly dependent upon the respiratory processes.

The best-known phosphorescent plants are certain forms of Bacteria which develop on the surface of fish and meat, and the mycelium, formerly described as "Rhizomorpha," of the Fungus *Agaricus melleus*. As further examples of spontaneously luminous Fungi may be cited *Agaricus olearius*, found growing at the foot of olive trees in South Europe, and other less familiar Agarics (*Ag. igneus, noctilucens, Gardneri*, etc.). The phosphorescence of decaying wood is also, without doubt, due to the growth of Fungi or Bacteria. Of plants taking part in the phosphorescence seen in water, the most important are the Alga, *Pyrocystis noctiluca*, certain *Peridineae*, and some luminous *Bacteria*. Their phosphorescence, according to observations on *Ceratium tripos* made by REINKE, is brought about by mechanical as well as by thermic and chemical stimuli (51).

The so-called phosphorescence of the Moss, *Schistostega*, and of some Selaginellas and Ferns, has nothing in common with actual phosphorescence, but is produced solely by the reflection of the daylight from peculiarly formed cells (Fig. 331). The phosphorescence observed in some sea-weeds results, on the other hand, from the fluorescence and opalescence of certain of their albuminous substances, or from the iridescence of their cuticular layers.

IV. Growth

The size which plants may attain varies enormously. A Mushroom seems immeasurably large in contrast with a *Micrococcus*, but inexpressibly small if compared with a lofty Californian *Sequoia*. A *Bacillus* of the size of a Mushroom, or a Mould-Fungus of the height of a *Sequoia*, are, with their given organisation, physiologically as inconceivable as a Mushroom with the minuteness of a *Micrococcus*. The size of an organism accordingly is an expression of its distinct individuality, and stands in the closest relation to structure and conditions of life, and in each individual varies within certain narrow limits.

However large a plant may be, and however numerous its cells, it nevertheless began its existence as a single cell, microscopically small and of the simplest structure. To attain its final size and perfect development it must grow, that is, it must enlarge its body and undergo differentiation. Even for the minute unicellular bacteria growth is essential, as they multiply chiefly by cell division. Each daughter cell must grow and attain the dimensions of the parent cell, or in a few years the capacity for existence itself will be lost through their continually decreasing size. It is in fact impossible to conceive of a plant where perfect development is not the result of growth. If a growing Oak or Cedar be compared with the single spherical egg-cell from which it has arisen, it is at once clear that by the term growth we mean not only an increase in volume, but include also a long series of various developmental stages, and external and internal modifications. A mere increase in volume does not necessarily imply growth, for no one would say that a dried and shrivelled turnip grows when it swells in water. On the contrary, active growth may be accompanied by a considerable loss of substance, as is shown by the sprouting of potatoes kept in a dark cellar. Water is lost through transpiration as well as organic substance through respiration, and yet the new shoots show true growth.

In the lower organisms growth is exhibited in its most simple form. In an Amœba or a Plasmodium growth is simply an increase in their substance; in a unicellular Alga or in a Fungus it means, in addition to this, an enlargement of their cell walls. In the higher plants the processes of growth are far more complicated and various, so that, according to SACHS, three chief phases of growth can be distinguished, which, however, are not sharply separated, but merge imperceptibly one into the other :—

1. The embryonic phase in which the rudiments of new organs are formed.
2. The phase of elongation of the already formed embryonal organs.
3. The phase of internal development and completion of the tissues.

The Embryonal Development of the Organs

Plants, in contrast to the higher animals, continually develop new organs. These arise either from tissues retained in their embryonic condition, as at the growing point, or they have their origin in regions which have already more or less completely attained their definite form. The leaves and shoots spring directly from the tissues of the growing point; the first lateral roots, however, make their appearance at some distance from the growing point, where a perceptible differentiation of the tissues has already taken place.

Leafy shoots may also take their origin from old and fully-developed tissues, which again assume an embryonic character, accompanied by an accumulation of protoplasm and renewed activity in cell division. But as this only occurs in exceptional cases, shoots which thus arise out of their regular order are termed ADVENTITIOUS.

The manner of the **Formation of New Organs at the Growing Point** has already been described in the morphological portion of this book. It is only necessary here to again call attention to the fact that the young organs, with few exceptions, develop in acropetal succession, so that the youngest is always nearest the apex.

The point from which new organs arise, and the number which develop, are chiefly dependent upon inherited internal disposition. External factors can, however, exert an effect in particular cases. The influence of such factors as light, gravity, chemical and mechanical stimuli, which at certain times in the later life of the tissues is of extreme importance, has usually but little effect on the embryonal development. Yet, on the other hand, the position of the first division wall of the germinating spore of *Marsilia* is determined by the action of gravity, and the direction of the first wall (as well as of the preceding nuclear division) in the spore of *Equisetum* and the ova of *Cystoseira barbata*, *Pelvetia*, and *Ascophyllum* among the *Fucaceae* is determined by its relative position to the light (^{52}).

In **Adventitious Formations**, on the contrary, the influence of external forces is often very evident, as, for example, in the formation of climbing-roots, which in the Ivy and other root-climbers are developed only on the shaded side of the stem. In the Alga *Caulerpa* the new leaf-like organs arise only on the illuminated side of the parent organ. It is, on the other hand, the force of gravity which excites the formation of roots on the under side of underground rhizomes. It is also due to gravity that the growing points of shoots are formed only from the upper side of the tubers of *Thladiantha dubia*, or that new twigs develop, for the most part, from the upper side of the obliquely growing branches of trees. Contact stimuli, on the other hand, determine the primary inception and point of development of the haustoria of *Cuscuta* (p. 207). The sexual organs of Fern prothallia are always developed on the side away from the light; that is, in normal conditions on the under side, but in case of artificial illumination on the upper side.

As a result of one-sided illumination and the stimulus of gravity, together with the favouring influence of moisture, the rhizoids spring only from the under side of the gemmæ of *Marchantia*, so that eventually the two originally similar sides assume an altogether different anatomical structure.

Many adventitious formations are the result of definite external causes; as, for example, the galls induced by the stings of insects and the deposits of animal eggs and larvæ (cf. p. 153).

The development of adventitious formations is especially induced by MUTILATION of plants. NEW FORMATIONS are in this manner produced at points from which they would never have arisen on the uninjured plants. In the case of Pelargoniums, Oleanders, Willows, and many other plants, it is possible to induce the formation of roots wherever the shoots are cut. In other plants, however, there seem to be certain preferred places, such as the older nodes, from which, under the same circumstances, roots develop. In like manner new shoots will appear in the place of others that have been removed. IN THE DEVELOPMENT

OF NEW FORMATIONS ON A MUTILATED PLANT THOSE VERY ORGANS ARISE, OR PREFERABLY ARISE, OF WHICH THE PLANT HAS BEEN DEPRIVED. Rootless shoots develop first of all new roots. Roots and root-stocks deprived of their shoots form first new shoots. In these processes there is manifested an internal reciprocity in the formative growth of organs, which has been termed the CORRELATION OF GROWTH.

Correlation of growth is often, also, very apparent in the normal development of the organs of uninjured plants. It is due to this that scales of buds are developed in their special form rather than as foliage leaves. For, as GOEBEL showed, it is possible by artificial means, as, for example, by the timely removal of the leaves of the parent shoot of *Aesculus*, *Acer*, *Syringa*, *Quercus*, or in the case of *Prunus Padus*, by cutting off the upper extremity of the shoots, to induce the formation of normal foliage leaves in the place of the scales. The vigorous growth which ensues in the fruit and in the fruit-coverings after fertilisation and development of the embryo in the ovule, affords another example of correlation; for, in case no fertilisation of the egg-cell occurs, all those changes which produce a ripe fruit from the flower do not take place; and, instead, another correlative process is manifested by which the now useless organs are discarded. Certain plants, especially those modified by cultivation, form an exception to this: in many varieties of banana, in the seedless mandarin, and in the variety of raisins known as sultana, etc., although no seeds capable of germination are produced, the formation of a so-called fruit is nevertheless continued. Even in these instances it is essential for the formation of fruit that there shall have occurred a previous pollination of the stigma, or the fertilisation of the ovules, which, however, do not mature. According to MULLER THURGAU (^{53}) the formation of seeds in grapes exerts an influence on the form, quantity, and quality of the succulent portion of the berry. In some few exceptional cases, however, as in the Fig, even this impetus to fruit formation is not necessary (^{54}). The manner of the formation of conducting tissues in plants, and also their anatomical development, are regulated by correlation. From these few instances it may be seen how the principle of correlation affects the most various of the vital processes, even under normal conditions, and how the harmonious development and function of the single members of the plant body are controlled by it.

The polarity manifested by plants should also be considered as a special example of the correlation existing between the different parts of the plant body. This polarity is particularly apparent in stems and roots, and finds its expression in the tendency of every small piece of a stem to develop new shoots from that end which was nearer the stem apex, while the roots take their rise from the other end. Pieces of roots in like manner send out roots from the end originally nearer their apex, and shoots from the end towards the stem.

In accordance with this principle, detached pieces of stems produce new shoots from their "shoot-pole," and injured roots new roots from their "root-pole." This polarity, particularly investigated by VÖCHTING and SACHS, supplemented according to GOEBEL by the nutritive current setting towards the wounded surface, makes itself apparent in even the smallest pieces of stems or roots, and may, in this respect, be compared to the magnetic polarity exhibited by every small piece of a magnet. Unlike poles of a plant may readily be induced to grow together, while like poles may only be brought to do so with difficulty, and then do not develop vigorously. As a result of such experiments, a radial polarity has also been recognised by VÖCHTING in stem and root tissue: thus, for instance, pieces of a stem or root, inserted in a lateral incision of a similar organ, become united with it, if they are so placed that the side originally outermost occupies the same relative position in the new organ, but if this position is altered no such union takes place. Leaves take, in respect to polarity, a special position, for they are not organically included within new formations derived from them. Thus, from the basal end of a leaf, an entire plant, with roots, stem, and leaves, may arise, while the regenerative leaf itself gradually dies. It is of especial interest to observe the effect of external influences upon the position of new formations, when they come into opposition to the internal disposition of the plants themselves. In this respect, the behaviour of different species varies greatly. In one, the internal factors predominate, that is, the new formations appear quite independently of external conditions; in another, the external influences of the moment prevail; but the internal disposition of the plant, when thus constrained for the time being, ultimately makes itself apparent and the new formations never develop vigorously. A willow twig, planted in a reversed position, with the shoot-pole in the ground, will produce roots, and from the root-pole may even produce shoots. These, however, usually soon die and their place is supplied by other stronger shoots arising from the shoot axis just above the roots. It is only by the most careful suppression of any such developments that the shoots from the root-poles may be kept alive. In so-called "weeping" trees, the formation of side branches from the upper side of the hanging branches is favoured by external conditions, but the internal polarity prevents their vigorous development, and those formed soon die. In the cultivation of grapes and fruit trees this peculiarity is utilised to produce short-lived, fruit-producing shoots by bending over the vines or training the branches of the trees in the cultivation of wall fruits. On the other hand, in some cases the internal polarity is easily overcome by external influences. It is sometimes sufficient merely to reverse the erect thallus of *Bryopsis*, one of the *Siphoneae*, to convert the former apical portion into a root-like tube which penetrates the substratum and fastens itself to the grains of sand. It has also been positively determined, although otherwise such cases are unknown among the higher plants, that the growing points of the roots of *Neottia* and of certain Ferns (*Platycerium*, *Asplenium esculentum*) may be converted through some inherent tendency into the vegetative cone of a stem (^{55}).

The correlation phenomena manifested in the formation of new organs have the greatest practical importance, for the propagation of plants by cuttings or grafting is based upon them.

In artificial reproduction detached pieces of plants are made use of for the purpose of producing a fresh complete plant. In many cases this is easily done, but in others it is more difficult or even impossible. The favourite and easiest method is by means of cuttings, that is, the planting of cut branches in water, sand, or earth, in which they take root (Pelargonia, Tradescantias, Fuchsias, Willows, etc.). Many plants may be propagated from even a single leaf or portion of a leaf, as, for instance, is usually the case with Begonias. The young plants spring from the end of the leaf-stalk, or from its point of union with the leaf-blade, or from the ribs, particularly when they are artificially broken or incised. In other cases the leaves, while still on the parent plant, have the power to produce adventitious buds, and, in this way, give rise to new plants (see Vegetative Reproduction). Even from roots or pieces of roots it is also possible to propagate some few plants. An example of this is afforded by *Ipecacuanha*, whose roots are cut in pieces and then sown like seeds. The Dandelion possesses the same capability of developing from small portions of the root, and to this peculiarity is due the difficulty with which it is destroyed.

In grafting or budding, cuttings from one plant are inserted in another, so that they grow together to form physiologically one plant. The union is accomplished by means of a callus (p. 142), formed by both the scion and the adopted stock. Vessels and sieve-tubes afterwards develop in the callus, and so join together the similarly functioning elements of both parts. Such an organic union is only possible between very nearly related plants, thus, for example, of the *Amygdalaceae*, the Plum, Peach, Almond, Apricot, may readily be grafted one upon the other, or of the *Pomaceae*, the Apple with the Quince ; but not the Apple with the Plum.

In spite of the apparent physiological union between the old stock and the newly-formed growth, from a morphological standpoint they lead an altogether separate and distinct existence. In its structural character, forms of tissues, mode of secondary growth, formation of bark, etc., each maintains it own individuality. In special cases it has been affirmed that they do mutually exert, morphologically, a modifying effect upon each other (Graft-hybrids), but this is doubtful. In practice several different methods of inserting cuttings are in use, but only the more important can be mentioned here.

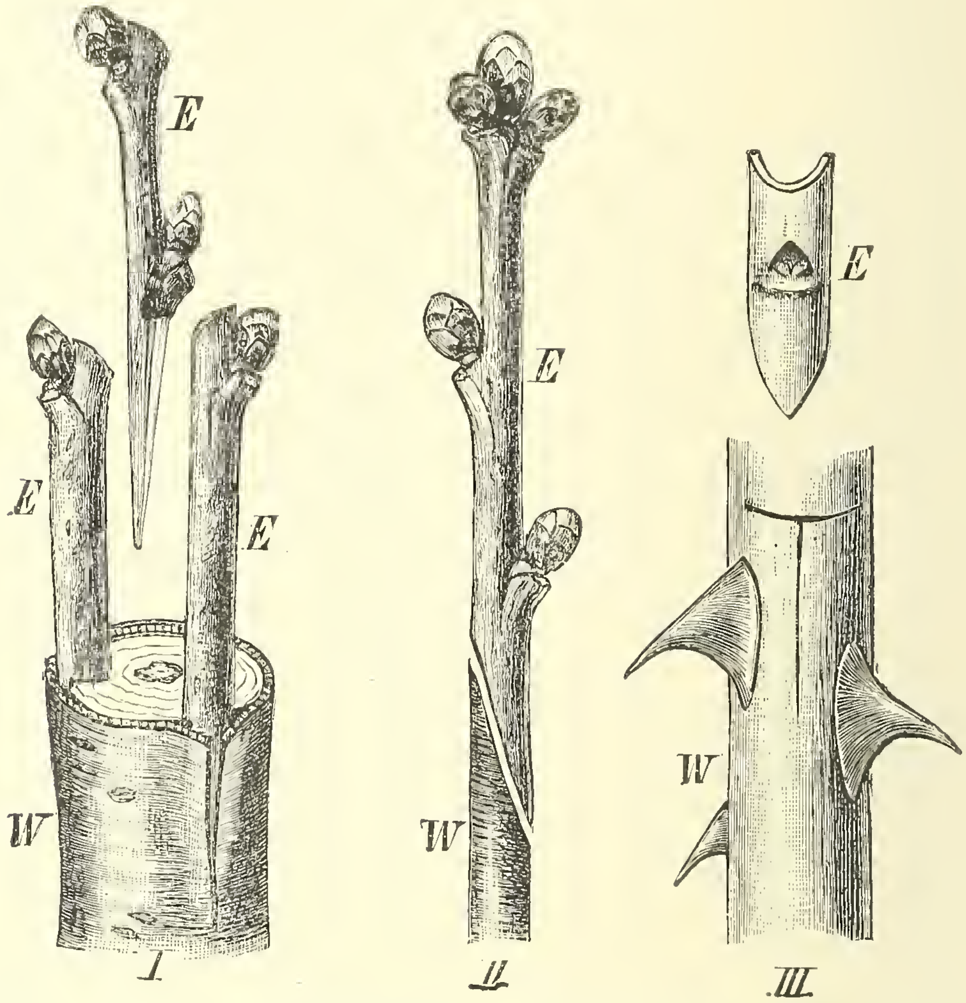


Fig. 194.—Different modes of grafting ; *I*, Crown grafting ; *II*, splice grafting ; *III*, bud grafting ; *W*, stock ; *E*, scion.

Grafting is the union of a shoot with a young and approximately equally-developed wild stock. Both are cut obliquely with a clean surface, placed together, and the junction protected from the entrance of water and fungi by means of grafting wax.

Cleft or tongue grafting is the insertion of weaker shoots in a stronger stock. Several shoots are usually placed in the cut stem of the stock, care being taken that the cambial region of the different portions are in contact, that the cortex of the shoots is in contact with that of the stock. In other methods of grafting the cut end of the shoot is split longitudinally and the cut shoot inserted in the periphery, or a graft may be inserted in the cortex or in the side of the stock. In grafting in the cortex the flatly-cut shoot is inserted in the space cut between the bark and the splint wood (Fig. 194, *I*). In lateral grafting, the shoot, after being cut down, is wedged into a lateral incision in the stock.

A special kind of grafting is known as BUDDING (Fig. 194, *III*). In this process a bud ("eye") and not a twig is inserted under the bark of the stock. The "eye" is left attached to a shield-shaped piece of bark, which is easily separated from the wood when the plants contain sap. The bark of the stock is opened by a T-shaped cut, the "eye" inserted, and the whole tightly covered. Occasionally some of the wood may be detached with the shield-shaped piece of bark (budding with a woody shield). In the case of sprouting buds, the budding is made in spring; in dormant buds, which will sprout next year, in summer.

The Phase of Elongation

For the performance of their proper functions, the embryonic rudiments of the organs must complete their external development. They must unfold and enlarge. This subsequent enlargement of the embryonic organs of plants is accomplished in a peculiar and economical manner. While the organs of animals increase in size only by a corresponding increase of organic constructive material and by the formation of new cells rich in protoplasm, and thus require for their growth large supplies of food substance, plants attain the chief part of their enlargement by the absorption of water—that is, by the incorporation of an inorganic substance which is most abundantly supplied to them from without, and to obtain which no internal nutritive processes are first necessary.

The great advantage resulting from this easy method of enlargement is apparent from a consideration of the importance of a large external surface for the nutrition of a plant. Assimilation is just so much the more productive, the larger the exposure of green surface, and the more accessible it is to the surrounding carbonic acid. In like manner, the superficial enlargement is exceedingly advantageous as regards the absorption of nourishment from the soil.

The absorption of water by living cells does not take place with the same rapidity and without interruption as in the case of porous bodies. Before the cells can take up additional water they must enlarge by actual processes of growth. The water, penetrating the young cells by imbibition or by the force of osmotic pressure, is uniformly distributed through the protoplasm, which fills the cell; in case the protoplasm is already abundantly supplied with water, it is instead accumulated in vacuoles (Fig. 58). As the vacuoles contain also organic and inorganic matter in solution, they exert an attractive force and give rise to further absorption of water. The sap of the vacuoles would, in turn, soon be diluted and its attractive force diminished, were it not that the regulative activity of the protoplasm soon provides for a corresponding increase of the dissolved salts, so that the concentration and attractive force of the sap are continually being restored or even increased. The separate vacuoles thus enlarged ultimately flow together into one large sap-cavity in the middle of the cell.

During this increase in the volume of the cell the protoplasm has experienced but little augmentation of its substance, or other modification. The enlargement of the cell has been almost wholly produced by the increased volume of water in the sap cavity, which, to distinguish it from the "nutrient water," "imbibition water," and "constitution water" of the plant, may be designated "inflation water."

As is often observed with the occurrence of many vital phenomena, the rate of distension of the walls with the inflation water is not uniform, but BEGINS SLOWLY, INCREASES TO A MAXIMUM RAPIDITY, AND THEN GRADUALLY DIMINISHING ALTOGETHER CEASES. As all the cells of equal age in an organ go through this process of inflation at the same time, the phenomena of increase and decrease in the rate of growth are apparent in the growth of the organ, and give rise to GRAND PERIODS OF GROWTH. Minor periods, or fluctuations in the rate of growth, occurring within the grand periods, are due to irregularities in the swelling of the cells, occasioned by change of temperature, light, and other influences operative on growth ([56]).

The large amount of water absorbed by the growing organ in the process of elongation does not lessen its rigidity, but, on the contrary, it is to the turgor thus maintained that the rigidity is due (cf. p. 163). Osmotic pressure seems also to take an important part in the growth of the cell wall itself. Cells in which the turgor is destroyed by a decrease in the water-supply exhibit no growth of their cell walls ; it is thus evident that the distension of the cell walls is physically essential for their surface-growth. This distension is in itself, however, by no means the cause of their growth ; the internal physiological conditions of the growth of the cell walls are dependent upon the vital activity of the living protoplasm. Without the concurrent action of the protoplasm, there is no growth in even the most distended cell wall ; on the contrary, active growth of the cell wall may take place with the existence of only a small degree of turgor tension. A correspondence between the turgor tension of the cell walls and the amount of growth cannot, under these conditions, be expected, nor can, on the other hand, the conclusion be drawn that turgor tension is inoperative in the processes of growth. The importance of the turgor tension is variously estimated, according to whether the growth of the cell wall is regarded as resulting from the interpolation of new particles of constructive material between the already existing particles of the cell-wall substance (INTUSSUSCEPTION) or to the plastic (*i.e.* inelastic, not resuming its original position) expansion of the distended cell wall. In the latter case the growing membrane would continually become thinner, and require to be strengthened by the deposition of new layers upon it (APPOSITION). Both processes, which may occur together, probably take part in the growth of cell walls. The necessity of a certain amount of turgor, if growth is to result from plastic stretching, is self-evident ; the stretching of the wall by the internal tension, though facilitating the introduction of the new particles in growth by intussusception, is, however, not so indispensable in this case.

The assumption of a growth by intussusception is intimately related to the views on the finer (or so-called molecular) structure of organic substances. The power of swelling in water, which may even lead to complete solution, exhibited by organic substances, shows that the water of imbibition does not merely penetrate into pre-existing capillary spaces, but makes a passage for itself by separating the solid particles from one another. It is further evident that these particles must be of minute (molecular) size. The intimate penetration of the water is the expression of a powerful molecular attraction, which is capable of exerting an enormous force; it is rendered possible by the peculiar molecular construction of organic substances, the cohesion of which is only gradually overcome by the water present in excess. The arrangement of the particles has been pictured as resembling a network or a honeycomb, while the frequent occurrence of double refraction as an optical property of organic substances has been explained as due to the crystalline structure and definite arrangement of the groups of molecules (micellae of NAEGELI) or to the relations of tension in a colloidal honeycomb-like system (BÜTSCHLI). The new cellulose particles would penetrate into the cell membrane, as particles of colouring matter may be introduced with the imbibition water into a colloidal organic substance (^{57}).

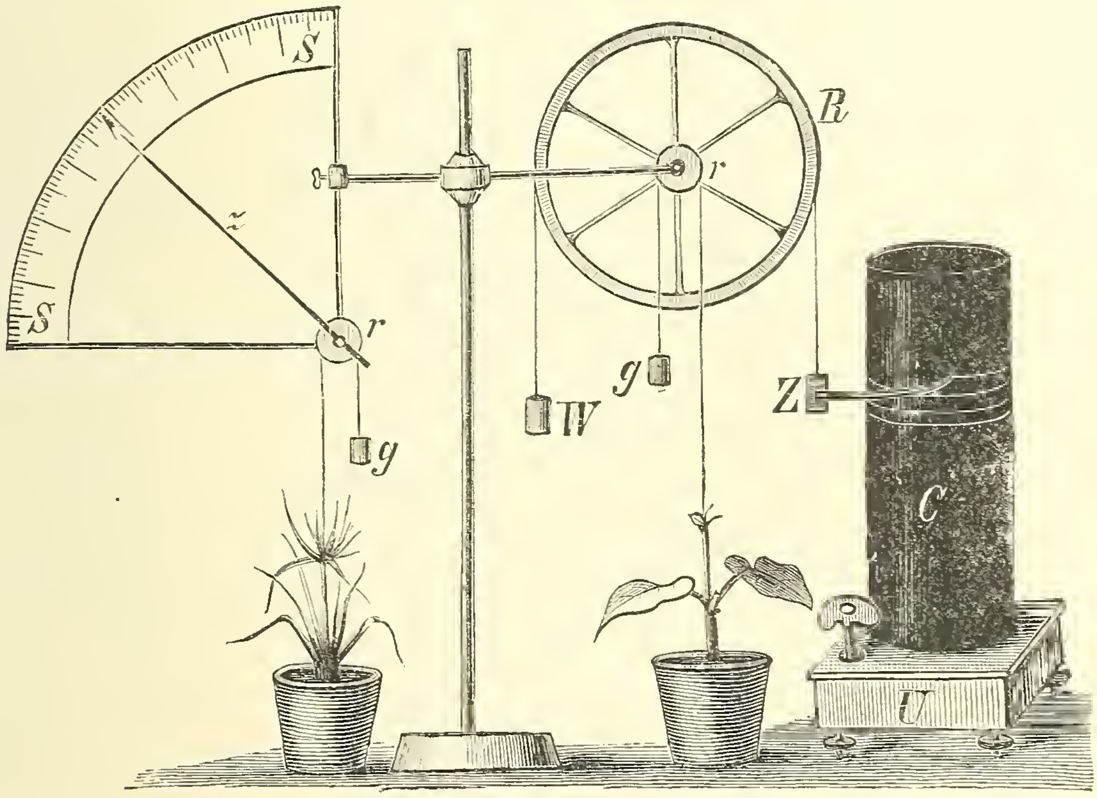


FIG. 195.—Simple and self-registering auxanometer. For description see text.

The process of elongation has so far been considered only in relation to the single cell, preparatory to the consideration of the phenomena presented by the growth of multicellular organs. With regard to this it is to be noted that the intensity of growth in two organs of equal total growth is greater the shorter the growing zone is.

The operations of growth in plant organs proceed very slowly; so slowly as to be, in general, imperceptible. The stamens, however, of many *Gramineae* grow so rapidly that their elongation is evident, even to the naked eye. An increase in length of 1·8 mm. a minute has been observed in the stamens of *Triticum* (Wheat). This approximately corresponds to the rate of movement of the minute-hand of a watch.

In comparison with it, the next known most rapidly growing organ is the leaf-sheath of the Banana, which shows an elongation of 1·1 mm., and a Bamboo shoot, an increase in length of 0·6 mm. per minute; while most other plants, even under favourable circumstances, attain but a small rate of elongation (0·005 mm. and less per minute) (58).

In order to measure the growth in length of a plant, it is customary to magnify in some way the actual elongation for more convenient observation. This may be effected by means of a microscope, which magnifies the rate of growth correspondingly with the distance grown. For large objects, the most convenient and usual method of determining the rate of growth is by means of an AUXANOMETER. The principle of all auxanometers, however they may differ in construction, is the same, and is based upon the magnification of the rate of growth by means of a lever with a long and short arm. In Fig. 195, at the left, a simple form of auxanometer is shown. The thread fastened to the top of the plant to be observed is passed over the movable pulley (*r*), and held taut by the weight (*g*), which should not be so heavy as to exert any strain on the plant. To the pulley there is attached a slender pointer (*Z*), which is twenty times as long as the radius of the pulley, and this indicates on the scale (*S*) the rapidity of the growth, magnified twenty-fold. By a growth in the length of the plant-stem of $\frac{1}{5}$ mm., the pointer would accordingly register 4 mm.

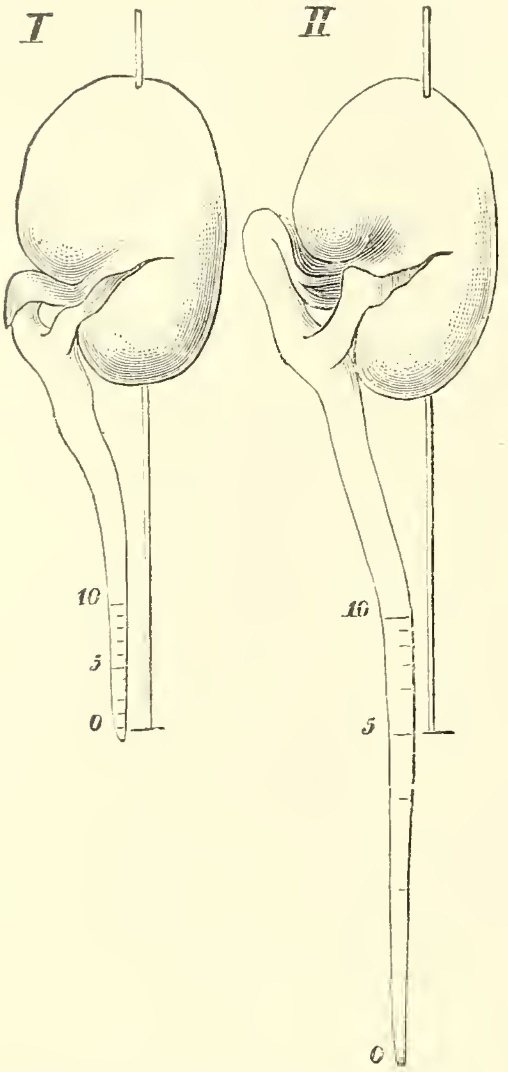


FIG. 196.—Unequal growth of different regions of the root-tip of *Vicia Faba*. *I*, The root-tip divided by marking with india-ink into 10 zones, each 1 mm. long. *II*, The same root after twenty-two hours; by the unequal growth of the different zones the lines have become separated by unequal distances. (After SACHS.)

Self-registering auxanometers are also used, especially in making extended observations. In Fig. 195, at the right, is shown one of simple construction. The radius of the wheel (*R*) corresponds to the long arm, and the radius of the small wheel (*r*) to the short arm of the lever, in the preceding apparatus. Any movement of the wheel, induced by the elongation of the shoot, and the consequent descent of the weight (*G*), is recorded on the revolving drum (*C*) by the pointer attached to the weight (*Z*), which is, in turn, balanced by the counterweight (*W*). The drum is covered with smoked paper, and kept in rotation by the clock-work (*U*). If the drum is set so that it rotates on its axis once every hour, the perpendicular distances between the tracings on the drum will indicate the proportional hourly growth.

The grand periods in the growth of an organ, due to the internal causes, are clearly shown by such self-registering auxanometers by the gradual increase and final decrease in the perpendicular distances, representing the increment of growth. STREHL found the daily growth in length of a root of Lupine, expressed in tenths of millimetres, to be: 58, 70, 92, 97, 165, 192, 158, 137, 122, 83, 91, 59, 25, 25, 8, 2, 0. For the first internode of the stem, growing in the dark, the daily growth observed was: 8, 9, 11, 12, 35, 43, 41, 50, 51, 52, 65, 54, 43, 37, 28, 18, 6, 2, 0.

The grand periods of growth, that is, the gradual increase from nil to a maximum, and the succeeding decrease to nil again, are, however, not evident throughout the whole of a root; during the growth in length only a small portion of a root is actually, at one time, in process of elongation. In roots of land plants the growing region extends over only about one centimetre of the extreme tip, often indeed over only ½ centimetre; while all the rest of the root has already completed its growth in length. The length of the growing region is influenced by such external conditions as mechanical hindrance, cold, warmth, dryness, etc., and exhibits consequent variations (59). That the grand period is exhibited by this short-growing region may be made clear by marking off with india-ink, near the tip of a root, narrow zones of equal width, which would thus also be made up of cells of nearly equal size. In Fig. 196, *I*, is shown a germinating Bean, *Vicia Faba*, whose root-tip has been marked in this way; Fig. 196, *II*, represents the same root after twenty-two hours of growth. The marks have become separated by the elongation of the different zones, but in different degrees, according to their position. The greatest elongation is shown by the transverse zone 3; from there the growth in length decreases towards the younger zones (2 and 1), as well as towards the older (4 to 10). This peculiar distribution of growth is but the result of the grand periods of growth of the cells in zones of different ages. In the millimetre-broad zones of a root of *Vicia Faba* Sachs found, after twenty-four hours, that the increase in growth, expressed in tenth-millimetres, was as follows:—

Zones: I., II., III., IV., V., VI., VII., VIII., IX., X., XI.
Increase: 15, 58, 82, 35, 16, 13, 5, 3, 2, 1, 0.

The elongating region in shoot axes is generally much longer than in roots, and usually extends over several centimetres, in special cases even over 50 or more centimetres. The distribution of the increase corresponds in stems, as in roots, with the grand periods of growth of the cells. Even by INTERCALARY GROWTH, where the region of elongation is not confined to the apex but occurs in any part of the organ, generally at its base (leaves and flower-stalks of many Monocotyledons), grand periods of growth are also apparent. A shoot of *Phaseolus multiflorus* which was divided, from the tip downwards, into transverse zones 3·5 mm. broad, showed in forty hours, according to Sachs,

in zones: I., II., III., IV., V., VI., VII., VIII., IX., X., XI., XII.
an increase of 20, 25, 45, 65, 55, 30, 18, 10, 10, 5, 5, 5
tenth-millimetres.

This periodicity in the growth in length occurs even when the external influences affecting growth remain unchanged, and is determined by internal causes alone.

External Influences upon Growth (60).—External factors often take an active part in the process of elongation, either as retarding or accelerating influences. As growth is itself a vital action, it is affected by any stimulus acting upon the protoplasm; on the other hand, as it is also a physical function, it is modified by purely physical influences. Growth is particularly dependent upon temperature, light, moisture, the supply of oxygen and other substances, and the existence of internal pressure and tension. It is also influenced by injuries.

The INFLUENCE OF TEMPERATURE is manifested by the complete cessation of growth at a temperature less than 0° or higher than

40°-50°. Between the MINIMUM and MAXIMUM temperatures, at which growth ceases, there lies an OPTIMUM temperature (p. 161), at which the rate of growth is greatest. This optimum temperature usually lies between 22° and 37° C. The three CARDINAL POINTS OF TEMPERATURE here given include a wide range, as they vary for different species and even for individual plants of the same species, and for their several vital processes. In tropical plants the minimum temperature may be as high as + 10° C., while those of higher latitudes, where the first plants of spring often grow through a covering of snow, as well as those of the higher Alps and polar regions, grow vigorously at a temperature but little above zero. In like manner, the optimum and maximum temperatures show great variation in different species of plants. It has been seen above that some *Algæ* and *Bacteria* grow in hot springs at a temperature of 80° C., which would be fatal to other plants. The optimum does not usually lie in the middle between the minimum and maximum, but is nearer the maximum.

A certain amount of variation in the temperature favours the germination of seeds more than exposure to a constant temperature, even when the latter is the optimum. The same appears to be the case with certain fungal spores (61).

The INFLUENCE OF LIGHT makes itself felt in a different manner from changes of temperature. Light as a general rule retards growth. This is apparent from observations on stems and roots grown in the dark, and is also true in regard to the growth of leaves, if the disturbing effects resulting from long-continued darkness be disregarded. Too great an intensity of light causes a cessation of the growth of an organ, while feeble illumination or darkness increases it. The effect of darkness upon the growth of plants is, however, differently manifested according to its duration, whether it be continuous, or interrupted, as in the changes of night and day. Long-continued darkness produces an abnormal growth, in that the growth of certain organs is unduly favoured, and of others greatly retarded, so that a plant grown altogether in the dark presents an abnormal appearance. The stems of Dicotyledons, in such case, become unusually elongated, also soft and white in colour. The leaf-blades are small and of a yellow colour, and remain for a long time folded in the bud (Fig. 197, *E*). A plant grown under such conditions is spoken of as "etiolated."

This diminution in the size of the leaf-blades and the elongation of the stem (and leaf-stalks) are not manifested by all plants, nor under all circumstances. The stems, for instance, of certain *Cacti* are much shorter when grown in the dark than in the light. Similarly, the leaves of varieties of the Beet (*Beta*) grow as large, or even larger, in the dark than in the light; this is also true, under conditions favourable to nutrition, of the leaves of other plants (*Cucurbita*). In the shade of a forest leaves often become larger than in full daylight. They are then proportionally thinner, and the palisade cells which, in leaves fully exposed to the light, are in close contact, become pointed below, and thus produce intercellular spaces between them. In this way the modifying influence of light of diminished intensity is apparent in the internal structure of such shade-leaves. Flowers, however, if sufficient constructive material be provided by the assimilating leaves, develop, according to SACHS' observations, as well in the dark as in the sunlight, except that they are sometimes paler in colour. If, however, the assimilatory activity of the green leaves be reduced or destroyed by depriving them of light, many plants, as VÖCHTING found, form only inconspicuous or cleistogamous flowers.

The tissues of etiolated stems and leaf-stalks are fuller of water and thinner-walled than in normally growing plants. Even the roots of such plants are often found to be less strongly developed. The supply of reserve material at the disposal of plants growing in the dark is utilised, together with the help of an unusual amount of inflation water, in the elongation of the axis. This elongation of the shoot axis, resulting from growth in darkness, is of especial value in the development of young plants from underground tubers, rhizomes, and seeds. When the leaves must themselves reach the light by their own elongation, as in many Monocotyledons, they act just as the stems of Dicotyledons, and attain an abnormal length in the dark.

From what has already been said it would seem that plants must grow more rapidly during the night than day, and this is actually the case where other conditions affecting growth remain the same by night as by day. A too low temperature during the night may, however, completely counteract the accelerating influence of darkness upon the growth.

Just as the rays of light of different wavelength and refrangibility were found to be of different value in the process of assimilation, so growth is by no means equal in differently-coloured light. IT IS TO THE STRONGLY REFRACTIVE, SO-CALLED CHEMICAL, RAYS THAT THE INFLUENCE OF LIGHT ON GROWTH IS DUE; the red-yellow end of the spectrum acts upon many plants in the same manner as darkness (62).

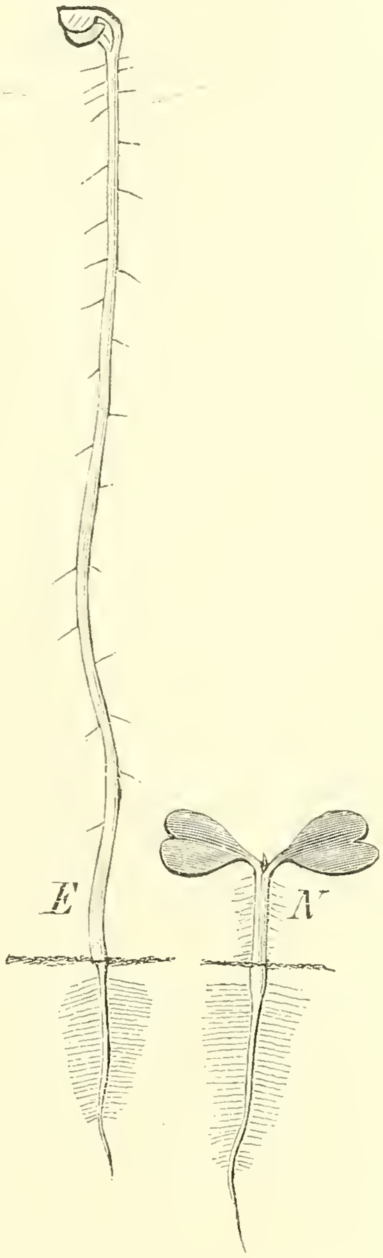


FIG. 197.—Two seedlings of *Sinapis alba*, of equal age: *E*, grown in the dark, etiolated; *N*, grown in ordinary daylight, normal.

MOISTURE exerts a twofold influence upon growth. It acts as a stimulus, and also, by diminishing transpiration, increases turgidity.

Plants in damp situations are usually larger than those grown in dry places, and in fact may differ from them in their whole habit and mode of growth. Direct contact with water seems frequently to exert a special influence upon the external form of plants. Amphibious plants, that is, such as are capable of living both upon land and in water, often assume in water an entirely different form from that which they possess in air. This variation of form is particularly manifested in the leaves, which, so long as they grow in water, are finely dissected, while in the air their leaf-blades are much broader (cf. Fig. 34). The leaf-stalks and internodes also often exhibit a very different form in air and water, and undergo the same abnormal elongation as in darkness. This is especially noticeable in submerged water plants, whose organs must be brought to the surface of the water (young stems and leaf-stalk of *Trapa natans*, stem of *Hippuris*, leaf-stalk of *Nymphaea*, *Nuphar*, *Hydrocharis*). Such plants are enabled by this power of elongating their stems or leaf-stalks to adapt themselves to the depth of the water, remaining short in shallow water and becoming very long in deep water.

The great importance of free OXYGEN has already been alluded to in connection with respiration (p. 217). Without gaseous or dissolved oxygen in its immediate environment the growth of a plant entirely ceases, at least in the case of aërobionts.

MECHANICAL INFLUENCE.—Pressure and traction exert a purely mechanical influence upon growth, and also act at the same time as stimuli upon it. External pressure at first retards growth; it then, however, according to PFEFFER, stimulates the protoplasm and occasions the distension of the elastic cell walls, and frequently also an increase of turgor. As a consequence of this increased turgor the counter-resistance to the external pressure is intensified. If the resistance of the body exerting the pressure cannot be overcome, the plasticity of the cell walls renders possible a most intimate contact with it; thus, for instance, roots and root-hairs which penetrate a narrow cavity so completely fill it that they seem to have been poured into it in a fluid state. It would be natural to suppose that the effect of such a tractive force as a pull would accelerate growth in length by aiding and sustaining turgor expansion. But the regulative control exercised by the protoplasm over the processes of growth is such that mechanical strain, as HEGLER has shown, first acts upon growth to retard it (except in the maximum of the grand periods), but then causes an acceleration of even 20 per cent. The elastic resistance and rigidity of cell walls are increased by the action of a strain; such a strain may also induce the formation of collenchyma and sclerenchyma which would not otherwise have been developed. Thus a leaf-stalk of *Helleborus*, which at first can just bear a weight of 400 grammes may have this gradually increased to 3500 grammes (63).

Rarefaction of the air, chemical stimuli, and internal states may exert considerable influence on growth. According to TOWNSEND, slight wounds accelerate growth, while more serious ones retard it.

The Internal Development of the Organs

The internal development of the organs is only completed after they have finished their elongation and attained their ultimate size. They are then first enabled to fully exercise their special function. To this end cell cavities usually become more or less fused, and the cell walls thickened, often in a peculiar and characteristic manner (p. 63).

In the case of plants equipped for a longer duration of life, a growth in thickness follows the growth in length (p. 122).

Periodicity in Development and Duration of Life

The periodically recurring changes in the determinative external influences, especially in light and temperature, occasioned by the alternations of day and night and of the seasons, cause corresponding periodical variations in the growth of plants. These variations do not follow passively every change in the condition of the external influences. On the contrary, the internal vital processes of plants so accommodate themselves to a regular periodicity that they continue for a time their customary mode of growth, independently of any external change. The nightly increase of growth, which is especially noticeable after midnight in the curve of growth, and the retardation of growth, specially marked after mid-day, will continue to be exhibited for some time in prolonged darkness when the temperature remains constant, thus under these conditions *Helianthus tuberosus* has been observed to continue its regular DAILY PERIODS for two weeks, affording an example of the inexplicable occurrence of so-called AFTER-EFFECTS, which are frequently mentioned in a later chapter.

Still greater is the influence exerted on the life of plants by the alternation of winter and summer, which in the plants of the colder zones has rendered necessary a well-marked winter rest. This is not in reality an absolute rest; for although the outwardly visible processes of development and growth stand still, the internal vital processes, although retarded, never altogether cease.

The ANNUAL PERIODS of growth occasioned by climatic changes, which are rendered so noticeable by the falling of the leaves in the autumn, and the development of new shoots and leaves in the spring, have stamped themselves so indelibly upon the life of the trees and shrubs of the temperate zones, that, when cultivated in tropical lands where other plants are green throughout the year and blossom and bear fruit, they continue to lose their leaves and pass for a short time at least into a stage of rest. The Oak, Beech, Apple, and Pear retain their resting period in the sub-tropical climate of Madeira, while, under uniformly favourable conditions in the mountain regions of Java, the periodicity may be disturbed in particular individuals. This even occurs in the several branches of the same tree which may then bear leafy and leafless boughs at the same time. Other trees again gradually accustom themselves to the new conditions, as the Cherry and Peach, for instance, which in Ceylon have become evergreen trees. The Peach is reported to produce flowers and fruit throughout the entire year; while the Cherry, like many other trees of the temperate zone, ceases altogether to bear flowers in tropical climates. Since in these tropical localities endemic species may exhibit well-marked periods of rest and of renewed vegetative activity, it is clear that such periodicity is not merely induced and regulated by external influences. Its cause must rather be sought in an autonomous, rhythmic course of the vital process itself. Although to so many plants winter is the season of rest and cessation from growth, other plants, *e.g.* certain Lichens and Mosses, seem to find in the warmer days of winter the most favourable conditions of vegetation; and in summer, on the contrary, either do not grow at all or only very little. Similarly, many spring plants attain their highest development, not in summer, but during the variable weather of March and April, and, for the most part, they have entered upon their rest period when the summer vegetation is just awakening.

In countries where there are alternate rainy and dry periods, the latter generally correspond to the winter period of vegetative rest.

The interruption of vegetative processes in meadow and field plants by repeated mowing has, according to WETTSTEIN, induced a seasonal dimorphism in many cases. The shoots developed in late summer differ considerably from those formed in the spring (64).

Favourable conditions may shorten the resting period, especially if the organisms have previously been exposed to the influence of frost, drought (withering), or, as JOHANNSEN discovered (65), to ether vapour, etc. This premature awakening does not, however, result equally readily at all periods of the resting time. It occurs best in the later portion of the latter, just before the normal time of awakening, and almost equally well in the earlier portion just after arrest has taken place. In the intervening period of complete rest such attempts are usually without result. These facts must be considered in the forcing of plants, as must also the fact of the temperature optima differing for the several developmental processes, for some of which they are relatively low.

DURATION OF PLANT LIFE.—The life of a plant, during the whole of its development, from its germination to its death, is dependent upon external and internal conditions. In the case of the lower vegetable organisms, such as Algæ and Fungi, their whole existence may be completed within a few days or even hours, and indeed some of the higher herbaceous plants last only for a few weeks, while the persistent shrubs and trees, on the other hand, may live for thousands of years.

After the formation of the seeds, there occurs in many plants a cessation of their developmental processes, and such a complete exhaustion of vitality that death ensues. Such an organic termination of the period of life occurs in our annual summer plants, which, according to KLEBS, can be made perennial by artificially preventing their reproduction. It also takes place with plants in which the preparatory processes for the formation of fruit have extended over two or more years, as in the case of the 10 to 40-year-old Agave, which, after the formation of its stately inflorescence, dies of exhaustion, and in some Palms. In plants, on the other hand, which in addition to the production of flowers and fruit accumulate also a reserve of organic substance, and, with their reproductive organs, form also new growing points, life does not cease with the production of the seeds. Such plants possess within themselves the power of unlimited life, the duration of which may only be terminated by unfavourable external conditions, the ravages of parasites, injuries from wind, and other causes.

The longevity of trees having an historical interest is naturally best known and most celebrated, although, no doubt, the age of many other trees, still living, dates back far beyond historical times. The celebrated Lime of Neustadt in Würtemberg is between 800 and 1000 years old; the age of the Fir of Béqué is estimated at 1200 years, and a Yew in Braburn (Kent) is at least as old. A stem of a *Sequoia* in the British Museum has, with 1330 annual rings, a diameter of 4·5 m., and, according to CARRUTHERS, must have originally been 28·5 m. in circumference. An *Adansonia* at Cape Verde, whose stem is 8-9 m. in diameter, and a Water Cypress, near Oaxaca, Mexico, are also well-known examples of old trees. Of an equally astonishing age must have been the celebrated Dragon-tree of Orotava, which was overturned in a storm in 1868, and afterwards destroyed by fire. The lower plants also may attain a great age; the apically growing mosses of the calcified *Gymnostomum* clumps, and the stems of the *Sphagnaceae*, metre-deep in a peat-bog, must certainly continue to live for many hundred years.

In thus referring to the ages of these giant plants, it must not be understood that all the cells remain living for so long a time, but rather that new organs and tissues are developed, which continue the life of the whole organism. All that is actually visible of a thousand-year-old Oak is at most but a few years old. The older parts are dead, and are either concealed within the tree, as the pith and wood, or have been discarded like the primary cortex. The cells of the original growing point have alone remained the whole time alive. They continue their growth and cell division so long as the tree exists; while the cells of the fundamental tissue arising from them, and destined for particular purposes, all lose their vitality after a longer or shorter performance of their functions.

The cells of the root-hairs often live for only a few days ; the same is also true of the glandular cells and trichomes of stems and leaves. The wood and bast fibres, as also the sclerenchymatous cells, lose their living protoplasm after a short time. Entire organs of long-lived plants have frequently but a short existence ; the sepals, petals, and stamens, for example. The foliage leaves, also, of deciduous trees live only a few summer months and then, after being partly emptied of their contents, are discarded. The leaves even of evergreen plants continue living but a few years, before they too fall off. Small twigs, especially of Conifers, are also subject to the same fate. The cells of the medullary rays afford the best examples of long-lived cells constituting permanent tissues. In many trees, as in the Beech, living medullary ray cells over a hundred years old have been found, although, for the most part, they live only about fifty years.

V. The Phenomena of Movement

In every living organism there is constantly occurring in the course of the metabolic processes an active movement and transposition of substance. As these movements are for the most part molecular they are generally imperceptible; but that they actually take place is demonstrated with absolute certainty by the local accumulation and diminution of substance, shown both by weighing and by the results of chemical analysis.

There are also other forms of movement which play an important part in the physiology of every organism, and on which its vital processes are to a large extent dependent: these are the movements due to heat and the related conditions of vibration resulting from light, electricity, etc.

Apart from the movements of this class, which may take place within organisms which, externally, are apparently at rest, there occur also in plants actual CHANGES IN POSITION, externally noticeable but usually of gradual operation; yet in special cases they may involve rapid motion. These movements may be carried on either by the whole plant or by single organs.

Reference is here made only to the SPONTANEOUS MOVEMENT resulting from the activity of a plant organism itself, and this should not be confused with the PASSIVE movements due to externally operating mechanical agencies, such as water and wind, which, although they have a certain importance for plant life, will not be here considered.

PROTOPLASM itself is capable of different movements. Naked protoplasmic bodies almost always show slow movements resulting in a gradual change of position; but cells enclosed by cell walls possess also the power of INDEPENDENT LOCOMOTION, often indeed to a considerable extent. Multicellular plants, however, as a rule ultimately attach themselves, by means of roots or other organs, to the place of germination, and so lose for ever their power of locomotion, except in so far as it results from growth. A gradual change in position due to growth is apparent in plants provided with rhizomes, the apical extremities of which are continually growing forward, while the older portions gradually die off. A yearly elongation of 5 cm. in the apical growth of the rhizomes would result, in twenty years, in moving the plant a distance of one metre from its original position. A seedling of *Cuscuta* (p. 207) in its search for a host plant illustrates the power of maintaining, for a time, a creeping movement over the surface of the soil; a growing *Caulerpa* (Fig. 253) likewise exhibits in the course of years a similar advancing movement. In addition to these movements, occasioned by a growth in length, plants firmly established in the soil possess also the power of changing the position and direction of their organs by means of CURVATURE and ROTATION. In this way the organs are brought into positions necessary or advantageous for the performance of their function. By this means, for example, the stems are directed upwards, the roots downwards; the upper sides of the leaves turned towards the light; climbing plants twined about a support, and the stems of seedlings so bent that they break through the soil without injury to the young leaves.

Movements of Naked Protoplasts and Single Cells

The creeping movements of naked protoplasts, such as are shown by an amœba or plasmodium, in the protrusion, from one or more sides, of protuberances which ultimately draw after them the whole protoplasmic body, or are themselves again drawn in (Fig. 198), are distinguished as AMŒBOID MOVEMENTS. These movements resemble, externally, the motion of a drop of some viscid fluid on a surface to which it does not adhere, and are chiefly due, according to BERTHOLD, to superficial tension, which the protoplasm can at different points increase or diminish, by means of its quality of irritability. (By means of irregular changes of surface-tension similar amœboid movements are also exhibited by drops of lifeless fluids.)

In the SWIMMING MOVEMENTS BY MEANS OF CILIA, on the contrary, the whole protoplasmic body is not involved, but it possesses special organs of motion in the form of whip-like FLAGELLA or CILIA. These may be one, two, four, or more in number, and arranged in various ways (Figs. 96, 97). They move very rapidly in the water and impart considerable velocity to the protoplast, often giving it at the same time a rotatory movement. While the swiftest ship requires 10-15 seconds to travel a distance equal to its own length, the velocity with which these protoplasmic bodies are impelled by their cilia, in a second, is two or three times their length, although, owing to their diminutive size, the distance travelled by them in an hour would amount to only about a metre. The protoplasmic body is conveyed by the motion of the cilia in a definite direction, which is so regulated by the action of stimuli that it may be instantly changed. In this way the direction and velocity of the ciliary movements are made serviceable to the protoplasmic organisms through the irritability of the protoplasm. Gravity and light, certain substances in solution, and mechanical hindrances are the principal influences which regulate the movements of free-swimming protoplasmic bodies and cells. The direction of the movements of the swarm-spores of Algæ are chiefly determined by the light. So long as they remain in darkness they move through the water in all directions; but as soon as they are illuminated from one side only, a definite direction in their movements is perceptible. They move either straight towards the light or turn directly away from its source. Their retrogressive movements from the light occur either in case of too intense illumination, or at a certain age, or through some unknown disturbing irritation. The advantage of such HELIOTACTIC MOVEMENTS (phototactic) is at once apparent when the part taken by the swarm-spore in the life of an Alga is considered. In order to provide for the future nutrition of the stationary Alga into which it afterwards develops, it must seek the light. If a point with suitable (that is, not too intense and not too weak) illumination be attained, then the swarm-spore must attach itself by the end which carries the cilia: to do this it must turn itself from the light towards a dark object. On the other hand, as the swarm-spores do not come to rest at all in absolute darkness, but swim continuously until thoroughly exhausted, the possibility of their attaching themselves in a spot devoid of light where the new plant could not assimilate is excluded.

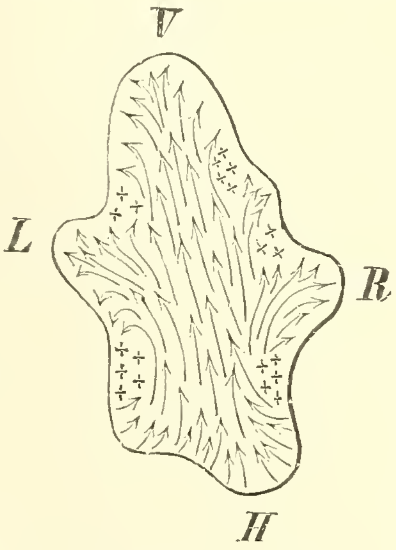


FIG. 198.—Amœboid movement. The arrows indicate the direction and energy of the movement; the crosses, the points at rest. At the time being the principal movement is from *H* to *V*, but at any moment it may be towards *R* or *L*, and so change the direction of the course taken by the amœba.

The SWARM-SPORES of water Fungi and motile Bacteria, according to PFEFFER'S investigations, are chiefly influenced in their movements by the unequal distribution of dissolved substances in their environment (chemotaxis). Minute traces of free oxygen can be recognised by the influence exerted on the movement of certain *Bacteria*; ENGELMANN'S bacterial method depends on this fact. According to their momentary requirements and their sensitiveness to stimuli, such small organisms move either towards or away from the points of highest concentration; they are sensitive to the quantity as well as the quality of the dissolved substances, and also to the osmotic effects of the latter (osmotaxis) [66].

As the result of similar CHEMOTACTIC MOVEMENTS spermatozoids approach the female sexual organs. PFEFFER has demonstrated that the spermatozoids of Ferns are enticed into the long necks of the archegonia by means of malic acid: while the archegonia of the Mosses attract the spermatozoids by a solution of cane-sugar. In such cases an extremely small quantity of dissolved substance is often a sufficient stimulus to call forth active chemotactic movements; a 0·001 per cent solution of malic acid suffices for the attraction of Fern spermatozoids. The movements of amœbæ and plasmodia are similarly induced by external influences. These naked protoplasts live not only in water (amœbæ), but also in moist substrata (plasmodia, amœbæ), and seem to possess the power of seeking out situations with more moisture, or of avoiding them (before the formation of spores): their movements are also influenced by the direction of currents in the water (rheotaxis). The term thigmotaxis or stereotaxis has been applied to the property of certain swarming cells, which are stimulated by mechanical contact to remain attached to the object around which they are swarming. This has been observed in spermatozoids of *Fucaceae* and in *Chromatium weissii*, a sulphur-bacterium. In cases where cells enclosed by cell walls (*Sphaerella pluvialis*) swim freely about by means of cilia, the cilia spring from the protoplasm and pierce the cell walls.

Diatoms and Desmids exhibit quite a different class of movements. The Diatoms glide along, usually in a line with their longitudinal axes, and change the direction of their movements by oscillatory motions. From the manner in which small particles in their neighbourhood are set in motion, it was concluded that special organs of motion probably protrude, like pseudopodia, through openings in their hard silicified shell. Recently these motile organs have been seen in some forms. According to O. MÜLLER the movement is set up by a current of protoplasm, which bursts through the raphe; this may become invested with a mucilaginous sheath. Corresponding to the differences in the construction of the membrane, differences in the motile apparatus are found in the group. The cells of *Desmidiaceae* attach themselves to the substratum by mucilaginous excretions, and effect their peculiar movements by local fluctuations in the mucilaginous layer. The advancing movements of the filamentous *Oscillarieae* and *Spirulinae* take place, according to CORRENS, in a mucilaginous sheath, but their mechanism is as little understood as that of the slow movements of *Spirogyra*.

The Movements of Protoplasm within Walled Cells

Although plants which are firmly attached and stationary exhibit no such locomotory movements, the protoplasm within their cells does possess a power of movement. Such internal protoplasmic movements are especially active in the non-cellular *Siphoneae*, in the elongated internodal cells of the *Characeae*, in the hairs of many plants, as well as in the leaf-cells of some aquatic plants. The active protoplasmic currents in *Caulerpa* move along its outer walls and around the internal cellulose bands, stretching from wall to wall in the manner of an immense imprisoned plasmodium.

The three following different forms of protoplasmic movement within cell cavities may be distinguished: CIRCULATION, ROTATION, and ORIENTATION.

In the case of CIRCULATORY MOVEMENT the different currents of protoplasm, although often quite close together, flow in different directions in slender protoplasmic strands, which stretch from the cell wall to the nucleus (cf. p. 57 and Fig. 60).

In the ROTATORY MOVEMENT the protoplasm moves along the cell wall in one direction only, dragging with it the nucleus and often also the chlorophyll grains (cf. p. 57).

The cause of these movements, which may take different directions in adjoining cells, and may also continue after the protoplasm has been drawn away from the cell walls by plasmolysis (p. 165), is not yet understood. It is, however, known that the continuance and activity of such protoplasmic movements, the existence of which was first observed by CORTI in 1772, and later rediscovered by TREVIRANUS in 1807, are dependent on factors which, in general, support and promote the vital activity; while the presence of free oxygen and proper conditions of temperature seem to be particularly favourable to them. That the movements in *Nitella* continued, according to KUHNE'S observations, for days and weeks in the absence of oxygen is explained, according to RITTER (67), by the power the *Characeae* possess of becoming facultative anaerobes. Through the study of sections in the cells of which currents had been induced in the protoplasm, by the injuries sustained in their preparation and by other abnormal conditions, grave errors have arisen concerning the existence of such protoplasmic movements in cells, in which under normal conditions they cannot be observed. The presence of protoplasmic currents in a cell may, in fact, indicate either an energetic vital activity, or, on the other hand, be merely a symptom of a pathological or, at least, of an excited condition of the protoplasm.

The movements of orientation of the protoplasmic body do not proceed in the same uninterrupted manner as the circulatory and rotatory movements. They are also usually so gradual as to be only recognisable through their operations. They are induced by changes in the external influences, especially as regards the intensity of the light, and result in producing a definite position of the protoplasmic bodies, as, for example, the orientation of the chlorophyll grains with regard to the light. Movements of this kind have been most frequently observed in Algæ, in submerged Duckweed (*Lemna trisulca*), in the prothallia of Ferns and Mosses; but similar movements can also be observed in the higher plants.

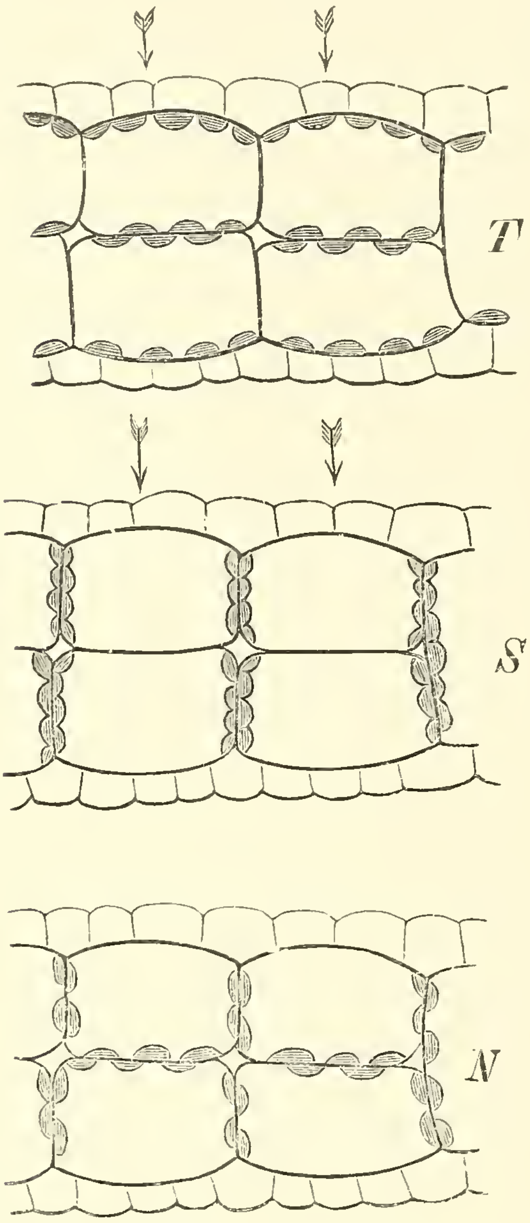


Fig. 199.—Varying positions taken by the chlorophyll grains in the cells of *Lemna trisulca* in illumination of different intensity. *T*, in diffuse daylight; *S*, in direct sunlight; *N*, at night. The arrows indicate the direction of the light. (After Stahl.)

Fig. 200.—Streaming protoplasm in the hyphæ of *Rhizopus nigricans*. (After J. C. Arthur.)

In the cells of the filamentous Alga *Mesocarpus*, the chloroplasts, in the form of a single plate suspended length-wise in each cell, turn upon their longitudinal axes according to the direction and intensity of the light. In light of moderate intensity, according to Stahl's observations, they place themselves transversely to the source of light, so that they are fully illuminated (transverse position); when, on the other hand, they are exposed to direct sunlight, the chlorophyll plates are so turned that their edges are directed towards the source of light (profile position). A similar protection of the chloroplasts against too intense light, and their direct exposure, on the other hand, to moderate illumination, is accomplished, where they are of a different form and more numerous, by their different disposition relative to the cell walls. In moderate light the chlorophyll bodies are crowded along the walls, which are transverse to the direction of the rays of light (Fig. 199, *T*). They quickly pass over to the walls parallel to the rays of light, however, as soon as the light becomes too intense, and so retreat as far as possible from its action (Fig. 199, *S*). In darkness or in weak light the chloroplasts group themselves in still a third way (Fig. 199, *N*), the advantage of which is not altogether clear.

The form of the chlorophyll bodies themselves undergoes modification during changes in their illumination ; in moderate light they become flattened, while in light of greater intensity they are rounded and thicker.

As a special mode of protection against too intense light, the chloroplasts of the *Siphoneae* (and the same thing is observed in many plants) become balled together in separate clumps. In correspondence with the changes in the position of the chloroplasts, the colouring of green organs naturally becomes modified. In direct sunshine they appear lighter, in diffused light a darker green. The attention of SACHS was first called to the phenomena of the movements of the chloroplasts by the accidental observation that the shadow of a thermometer was represented in dark green on a leaf otherwise directly illuminated by the sun.

Wounds and one-sided cell-wall thickenings likewise give rise to orientation movements, as they occasion a crowding together on one side of the nucleus and protoplasm.

A special mode of protoplasmic movements, which may be termed STREAMING, occurs, according to ARTHUR, in the mycelium of some *Fungi*. In it the whole mass of protoplasm, with its included vacuoles, streams towards the end of the hypha, only the limiting layer remaining at rest. After a longer or shorter interval a similar streaming movement sets in in the opposite direction (cf. Fig. 200).

CHARLOTTE TERNETZ observed the same type of movement in the mycelium of *Ascophanus carneus*, where the protoplasmic stream, with its vacuoles, makes its way through the pores of the perforated transverse septa. In this latter case it was established that the direction of the streaming was determined by local differences in the supply of water (68).

Movements producing Curvature

The movements of the organs of stationary plants, unicellular as well as multicellular, are accomplished by means of curvatures. In an organ that has grown in a straight line the longitudinal sides are all of equal length ; in an organ that is curved, however, the concave side is necessarily shorter than the convex side. When, accordingly, the opposite sides of a pliable organ become of unequal length, the organ must curve toward the shorter side (Fig. 169). Inequality in the length of the opposite sides may result from various causes. A curvature occurs if the length of one side remains constant, while the opposite side becomes shorter or longer, and also from the unequal elongation or contraction of both sides, and similarly from the elongation of one side and the contraction of the other.

Such curvatures most frequently occur in plants as a consequence of UNEQUAL GROWTH. More rarely they are due to the different length of the opposite sides, resulting from unequal TURGOR TENSION. A third source of curvature is found in the unequal amount of water taken up by IMBIBITION, and the consequent unequal distension of the cell walls on the opposite sides of an organ. A fourth cause is the loss of water from certain arrangements of cells, the latter being made to contract in a definite direction owing to the COHESIVE FORCE of the water which remains in them.

1. Movements dependent on Imbibition and Cohesion

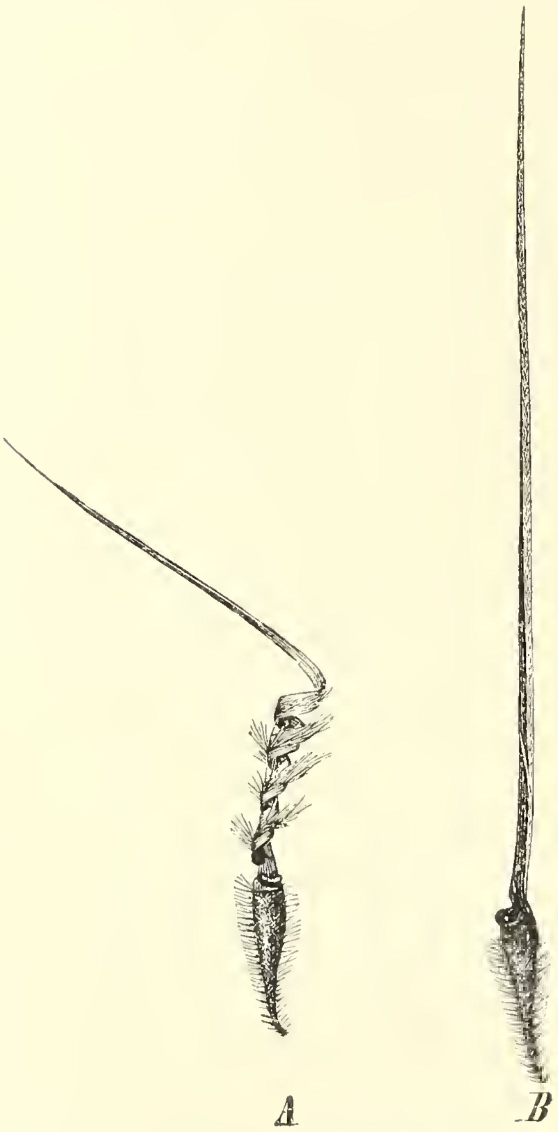


FIG. 201.—Fruit of *Erodium gruinum*. *A*, in the dry condition, coiled ; *B*, moist and elongated.

As the cell walls of actively living cells are always completely saturated with imbibition water, hygroscopic curvatures are exhibited only by dry and, for the most part, dead tissues. The hygroscopic movements in any case, however, are due to the physical properties of the cell walls, and have no direct connection with the vital processes, except in so far as the capacity of cell walls to swell and take up large quantities of imbibition water is due to the protoplasm by which they were formed. The activity of the protoplasm in the formation of the cell walls is likewise manifested in their anatomical structure, in their stratification and striation, and in the position of the pits, as well as in the arrangement and disposition of the cells themselves.

The absorption of imbibition water by cell walls is accompanied by an increase in their volume, and conversely the volume of the cell walls is diminished by the evaporation of the imbibition water. Accordingly, whenever unequal amounts of water are held by the cell walls on the different sides of an organ, either through unequal absorption or evaporation, hygroscopic movements are produced, which result in the curvature of the organs. In many cases the organs of plants are especially adapted to such movements, by means of which, in fact, important operations are often accomplished, as, for example, the dehiscence of seed-vessels and the dissemination and burial of seeds.

The rupture of ripe seed-vessels, as well as their dehiscence by the opening of special apertures (*Papaver*, *Lychnis*, *Antirrhinum*, etc.), is a consequence of the unequal contraction of the cell walls due to desiccation. At the same time, through the sudden relaxation of the tension, the seeds are often shot out to a great distance (*Tricoccae*, etc.). In certain fruits not only curvatures but torsions are produced as the result of changes in the amount of water they contain, *e.g. Erodium gruinum* (Fig. 201), *Stipa pennata*, *Avena sterilis*, by means of which, in conjunction with their stiff barb-like hairs, the seeds bury themselves in the earth.

The variation in dampness of the air causes the pappus hairs of the *Cynareae* (*Compositae*) to expand in dry and fold together in damp weather. The opening of the moss sporogonium is, in like manner, due to the hygroscopic movements of the teeth of the peristome. In the case of the *Equisetaceae* the outer walls of the spores themselves (the perinium) take the form of four arms, which, like elaters, are capable of active movements, by means of which numbers of spores become massed together before germinating, and the isolation of the diœcious prothallia prevented.

In order to call forth imbibition movements the actual presence of liquid water is not necessary; for, through their hygroscopicity, cell walls have the power of absorbing moisture from the air. They are hygroscopic, and for this reason the ensuing movements are also often termed hygroscopic movements.

STEINBRINCK and KAMERLING have distinguished the mechanisms which depend on the cohesive power of water from those depending on imbibition. The cohesion mechanisms were previously confounded with the latter, from which they differ in that, even during the movement, the cell walls remain saturated with water. It is the lumen of the cell which diminishes in size when the loss of water, on which the movement depends, occurs. The cohesive force of the remaining water tends to pull the thinner walls of the cell inwards after it, and thus to approximate other walls, which are strongly thickened and exhibit a definite arrangement. In this way an energetic shortening of the specialised tissue is brought about which leads to alteration of form or to the dehiscence of spaces enclosed by the tissue. The walls of anthers and of the sporangia of the higher cryptogams afford examples of such a method of dehiscence. The movements of the elaters of Liverworts and *Myxomycetes*, which serve to distribute the spores, as well as of the pappus of most, and the involucre of some, *Compositae*, are effected in the same way ([69]).

Mechanisms dependent on imbibition and on cohesion may co-operate in the movements of some plants. This is the case in the changes of form dependent on drying and wetting exhibited by plants which can endure without injury periods of desiccation, *e.g. Selaginella lepidophylla* (p. 177) and certain Mosses and Lichens.

2. Growth Curvatures

Movements from which curvatures result are, for the most part, produced by the unequal growth of living organs. The unequal growth is due, partly to internal causes which are still undetermined, and partly to the operation of external influences which can be positively demonstrated and defined. The movements resulting in the first case are spontaneous, and are called AUTONOMIC MOVEMENTS or NUTATIONS; in the second case the movements are the result of external stimuli, and are distinguished as irritable or PARATONIC MOVEMENTS.

Autonomic Movements are most plainly apparent in young actively-growing organs, although nutations have been shown to be exhibited by all growing plants, as their tips do not grow forward in a straight line, but, instead, describe irregular elliptical curves. These movements, which Darwin termed CIRCUMNUTATIONS, while often not perceptible to the eye, are very noticeable in some special organs.

The unfolding of most leaf and flower buds, for example, is a nutation movement which, in this instance, is induced by the more vigorous growth of the inner side of the young leaves. The same unequal growth manifests itself most noticeably in the leaves of Ferns and many *Cycadeae*. In the same manner, movements of nutation are caused in other lateral organs when growth is more energetic on either the upper side (EPINASTY) or on the lower side (HYPONASTY). The stems of many seedlings are, on their emergence from the seeds, strongly curved. From the nutation of the shoots of *Ampelopsis quinquefolia* a curvature is produced which continuously advances with the increased growth; so that, by means of its hooked extremity, a shoot is better enabled to seek out and cling to a support. When the unequal growth is not confined to one side, but occurs alternately on different sides of an organ, the nutations which result seem even more remarkable. Such movements are particularly apparent in the flower-stalk of an Onion or of *Yucca filamentosa*, which, although finally erect, in a half-grown state often curves over so that its tip touches the ground. This extreme curvature is not, however, of long duration, and the flower-stalk soon becomes erect again and bends in another direction. Thin and greatly elongated organs must, from purely physical reasons, quickly respond to the effects of unequal growth. The thread-like tendrils of many climbing plants, so long as they are in a state of active growth, afford excellent objects for the observation of nutation movements. If the line of greatest growth advances in a definite direction around the stem, its apex will exhibit similar rotatory movements (REVOLVING NUTATION). This form of nutation is characteristic of the tendrils and shoots of climbing plants, and renders possible their peculiar mode of growth. The SO-CALLED REVOLVING NUTATION OF TWINING PLANTS is not an AUTONOMIC MOVEMENT, and will be considered later with the paratonic movements.

Paratonic Movements.—The phenomena of paratonic movements are of the very greatest importance to plant life, for through their operations the organs of plants first assume such positions in the air, or water, or in the earth as are necessary for the performance of their vital functions. A green plant which spread its roots over the surface and unfolded its leaves below ground could not exist, even though all its members possessed the best anatomical structure. Seeds are not always so deposited in the soil, with the embryonal stem directed upwards and the radicle downwards, that their different organs can, merely by direct growth, attain at once their proper position. A gardener does not take the trouble to ascertain, in sowing seed, if the end which produces the root is directed downwards or the stem end upwards, he knows that in any position the roots grow into the ground and the stems push themselves above the surface. Plants must accordingly have in themselves the power of placing their organs in positions best adapted to the conditions of their environment. That is only possible, however, when the externally operative forces and substances, *e.g.* light, gravity, humidity, the presence of oxygen, can so influence the growth of a plant that it is constrained to take certain definite directions.

The same external influences excite different organs to assume quite different positions. Through the influence of gravity, the tap-root grows directly downwards in the soil, while the lateral roots take a more or less diagonal direction. The main stem grows perpendicularly upwards; it, like the primary root, is ORTHOTROPIC. The lateral branches, on the other hand, just as the secondary roots, assume an inclined position and are PLAGIOTROPIC. The apical extremities of shoots are constrained to seek the source of light; the leaves, on the contrary, under the same influence place their surfaces transversely to the direction of the rays of light. The different positions assumed by an organ when acted upon by external influences has been termed by SACHS ANISOTROPY. In addition to the purely morphological structure of the plant body, anisotropy also determines essentially its external form and appearance (70).

That all these paratonic movements cannot result merely from the action of external forces alone will be at once recognised if it be taken into consideration that anisotropic but in other respects similar organs are affected differently by the same influences, and that even the same organs react differently at different ages; and that, moreover, the external forces produce effects which bear no relation to their usual physical and chemical operations. It will, on the contrary, be at once apparent that they are rather the result of definite processes of growth, arising from an irritability to stimuli induced by external influences (cf. p. 160).

In order that external influences may produce such effects, plants must be sensitive to stimuli, that is, the stimuli must produce in them certain modifications with which, in turn, certain definite vital actions are connected. The precise manner in which an external influence produces an internal stimulation within an organism is not at present known. In order that an external physical force can operate as a stimulus, there must exist within the living substance definite structures or organs which are influenced by it. The movements of growth occasioned by external stimuli are, for the most part, movements in response to directive stimuli which lead to a definite position of the organ, relatively to the direction of the operative influence. The principal external stimuli that come into consideration are light (and electricity), heat, gravity, chemical influences (oxygen, nutritive substances, water, etc.), impact and friction.

As the points of greatest irritability in plants or their organs are often more or less removed from the points where the effect of the stimulation is manifested, a propagation of the stimulation must take place. Thus, a stimulus received by a non-motile organ may be conveyed to an organ capable of motion, and there produce movement. In the case of roots, for example, the geotropic stimulus is received by the non-motile root-tip, while the movement is induced in the part of the root in process of elongation ([71]).

The capacity of organs to assume a definite direction by means of curvatures of growth is distinguished, according to the nature of the particular inciting stimulus, as heliotropism, geotropism, hydrotropism, etc.; and these again are either POSITIVE or NEGATIVE, according as the direction taken by the curvature is towards or away from the irritating stimulus; while plant organs which place themselves more or less transversely to the line of action of the operative forces are termed DIATROPIC. As a special result of diatropism, a transverse position is assumed which is exactly at right angles to the direction in which the influence which acts as the stimulus is exerted. Dorsiventral organs, in particular, exhibit a tendency to assume diatropic and even transverse positions.

A. *Heliotropism*

The importance of light to plant life is almost incalculable. It is not only absolutely essential for the nutrition of green plants, but it has also a powerful effect upon the growth and general health of the plant organs. Deprived of light for any length of time, leaves and flowers usually fall off; fully developed, vigorous organs of green plants soon become yellow in the dark, and droop and die. Prolonged darkness acts like a poison upon those portions of plants accustomed to the light. On the other hand, exactly the reverse is true of plants or organs whose normal development is accomplished in darkness. Upon them the light has a most injurious, even fatal, effect, as may be easily observed in the case of Fungi and Bacteria. The hygienic importance of daylight in dwelling-places is due to the destructive action of light upon such forms of plant life. That some plants seek the light, while others avoid it, is not surprising in view of the adaptability which organisms usually exhibit in respect to the influences with which they come in contact in the natural course of their development.

A good opportunity for the observation of heliotropic phenomena is afforded by ordinary window-plants. The stems of such plants do not grow erect as in the open air, but are inclined towards the window, and the leaves are all turned towards the light as if seeking help. The leaf-stalks and stems are accordingly POSITIVELY HELIOTROPIC. In contrast with these organs the leaf-blades take up a position at right angles to the rays of light in order to receive as much light as possible. They are diaheliotropic, or TRANSVERSELY HELIOTROPIC, in the strictest sense (Fig. 202). If among the plants there should be one with aerial roots, *Chlorophytum* for instance, an example of NEGATIVE HELIOTROPISM will be afforded, as the aerial roots will be found to grow away from the window and turn towards the room.

For more exact investigation of heliotropic movements it is necessary to be able to control more accurately the source and direction of the light. This can be best accomplished by placing the plants in a room or box, lighted from only one side by means of a narrow opening or by an artificial light. It then becomes apparent that the direction of the incident rays of light determines the heliotropic position; every alteration in the direction of the rays produces a change in the position of the heliotropic organs. The apical ends of positively heliotropic organs will be found to take up the same direction as that of the rays of light.

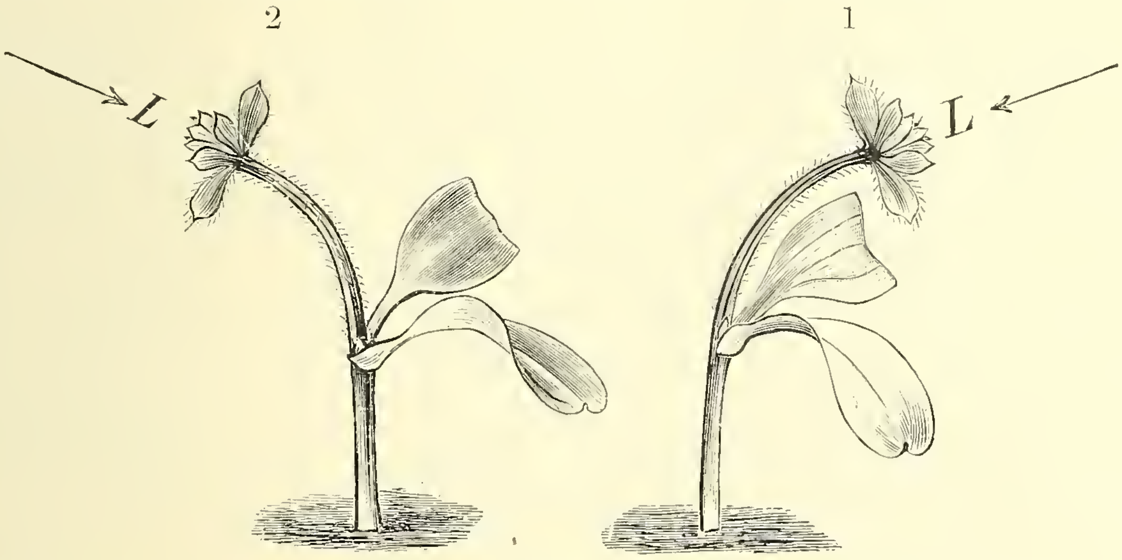


FIG. 202.—Heliotropic curvature of a seedling of *Galium Aparine*, resulting from one-sided illumination; in 1 the apex is in a line with the direction of the light, the leaves at right angles to it; in 2, with the illumination from the opposite direction, the same plant has quickly changed the position of its apex, while the cotyledons are only beginning to assume their heliotropic position. (Somewhat enlarged.)

The exactness with which this is done is illustrated by an experiment made with *Pilobolus crystallinus*. The sporangiophores of this Fungus are quickly produced on moist horse or cow dung. They are positively heliotropic, and turn their dark sporangia towards the source of light. When ripe these sporangia are shot away from the plant, and will be found thickly clustered about the centre of the glass covering a small aperture through which the light has been admitted; a proof that the sporangiophores were all previously pointed exactly in that direction (^{72}).

Upon closer investigation of the manner in which the POSITIVE HELIOTROPIC CURVATURE of an organ is accomplished, it is found THAT THE SIDE TURNED TOWARDS THE LIGHT GROWS MORE SLOWLY, THE SIDE AWAY FROM THE LIGHT MORE RAPIDLY THAN WHEN ILLUMINATED FROM ALL SIDES. This may be readily shown by previously marking with Indian ink regular intervals from one to two millimetres apart on the opposite sides of the organ. After the curvature has taken place the intervals between the marks will be found to be much farther apart on the shaded side than on the side turned to the light. As compared with the elongation under normal conditions of growth, the marks on the illuminated side have remained nearer together, while those on the shaded side have drawn farther apart; that is, the growth in the case of a positive heliotropic curvature has been retarded on the illuminated side and promoted on the shaded side. It also becomes evident, from observation of the ink-marks, THAT CURVATURE TAKES PLACE ONLY IN THE PORTIONS OF STEMS STILL IN PROCESS OF GROWTH, AND THAT THE CURVATURE IS GREATEST WHERE THE GROWTH IS MOST VIGOROUS (Fig. 202).

It was formerly believed that the increased growth of the shaded side was produced by the beginning of etiolation, and that the diminished growth on the illuminated side was due to the retarding effect which light exerts upon growth in length (p. 234). Other heliotropic phenomena were found to be at variance with this explanation of heliotropism. Unicellular perfectly transparent Fungus hyphæ are also subject to positive heliotropic curvature, although in this instance there can be no shaded side; on the contrary, the side of a hypha turned away from the light is especially illuminated on account of the refraction of the light rays. The fact, too, that negative heliotropic curvatures also take place renders it evident that heliotropism cannot be due to one-sided etiolation; for in negative heliotropism the side most directly illuminated is the one that grows more rapidly, although the retarding effect of light on the normal growth in length of negatively heliotropic organs is equally operative (roots, rhizomorpha).

It is evident from these considerations that it is not the difference in the intensity of the light which causes the heliotropic curvatures, but the direction in which the most intense light rays enter the organs. LIGHT ACTS AS A MOTORY STIMULUS WHEN IT PENETRATES AN ORGAN IN ANY OTHER DIRECTION THAN THAT WHICH CORRESPONDS WITH THE POSITION OF HELIOTROPIC EQUILIBRIUM

The heliotropic curvatures are most strongly produced, just as in the case of the heliotactic movements of freely moving swarm-spores, by the blue and violet rays, while red and yellow light exerts only an extremely slight influence, or none at all. It is due to the fact that the red-yellow and blue-violet rays are always present together in daylight, that the heliotropism of the leaves is of advantage to their assimilatory activity. Intermittent illumination has a more powerful effect on the plant than light of uniform intensity.

Sensibility to heliotropic influences is prevalent throughout the vegetable kingdom. Even organs like the roots of trees, which are never under ordinary circumstances exposed to the light, often exhibit heliotropic irritability. Positive heliotropism is the rule with aerial vegetative axes. Negative heliotropism is much less frequent; it is observed in aerial roots, and sometimes also in climbing roots (Ivy, *Ficus stipulata*, *Begonia scandens*), in the hypocotyl of germinating Mistletoe, in many, but not all, earth roots (*Sinapis*, *Helianthus*), in tendrils (chiefly in those with haptera or holdfasts), and in the stems of some tendril-climbers. By means of their negative heliotropic character, the organs for climbing and attachment turn from the light towards their support, and are pressed firmly against it.

Negative heliotropic curvatures are occasionally produced, not in the region of most rapid growth, but in the older and more slowly growing portions of the stem. The stems of *Tropaeolum majus*, for example, exhibit positive heliotropic curvatures in the region of their greatest elongation ; but lower down the stems, with the retardation of their growth, they become negatively heliotropic.

TRANSVERSE HELIOTROPISM is confined almost solely to leaves and leaf-like assimilatory organs, such as Fern prothallia and the thalli of Liverworts and Algæ. In these organs transverse heliotropism, in conformity with its great utility for assimilating, predominates over all other motory stimuli. Thus it is possible to cause the leaf-blades of a *Malva* or a *Tropaeolum* to turn completely over by illuminating their under surfaces by means of a mirror.

In too bright light the transverse position of the leaves becomes changed to a position more or less in a line with the direction of the more intense light rays. In assuming a more perpendicular position to avoid the direct rays of the mid-day sun, the leaf-blades of *Lactuca Scariola* and the North American *Silphium laciniatum* necessarily take the direction of north and south, and so are often referred to as COMPASS PLANTS. (As regards the vertical position of phyllodes, in connection with which may be mentioned the vertically-placed leaves of many *Myrtaceae* and *Proteaceae*, see p. 193) (73).

The heliotropic character of organs may change through the activity of external influences, and also at different stages of their development and growth. The youngest portion of the shoots of Ivy and *Tropaeolum* are positively heliotropic, while the lower and older portions turn away from the light. The flower-stalks of *Linaria cymbalaria* are at first positively heliotropic. After pollination, however, they become negatively heliotropic, and as they elongate they push their fruits into the crevices of the walls and rocks on which the plant grows.

The intensity of the illumination has a great influence since plants, which in subdued light are positively heliotropic, exhibit negative heliotropism when the illumination is excessive. Between the two reactions a neutral aheliotropic condition exists. OLTMANNS, who elucidated this variation of the reaction with the intensity of the light, and the search for an optimal intensity which is connected with it (cf. heliotactic swarm-spores, p. 241), termed it PHOTOMETRY. It remains to be noted that it is not so much the absolute intensity of the light which is of importance, but that the degree of change in light intensity needed to alter the reaction of the plant depends on the illumination to which the latter has been previously exposed (74).

B. *Geotropism*

That the stems of trees and other plants should grow upwards and their roots downwards, is such a familiar occurrence and so necessary for the performance of their respective functions as to seem almost a matter of course. Just as in the discovery of gravitation, it required an especially keen spirit of inquiry to lead to the investigation of this everyday phenomenon. The fact that everywhere on the earth, even on the sides of the steepest mountains, stems take a perpendicular direction; and that, while buried in the earth, this same direction is assumed with certainty by germinating seeds and growing shoots; and chiefly the fact also that a shoot, when forced out of its upright position, curves energetically until it is again perpendicular, led to the supposition that the cause of these phenomena must be in a directive force proceeding from the earth itself. The correspondence in the behaviour of a stem in always assuming a perpendicular position, with the continued maintenance of the same direction by a plumb-line, suggested at once the force of gravitation, and the English investigator KNIGHT, in 1809, demonstrated that the attraction of gravitation, in fact, exerted an influence upon the direction of growth. As KNIGHT was not able to nullify the constantly operative influence of gravity upon plants and so directly prove its influence, he submitted them to the action of centrifugal force—an accelerative force operating like gravity upon the masses of bodies, and which had, in addition, the advantage that it could be increased or diminished at will. KNIGHT made use of rapidly rotating, vertical wheels, upon which he fastened plants and germinating seeds in various positions. The result of his experiments was that the stems all turned towards the centre of the wheel and the roots directly away from it. On wheels rotating in a horizontal plane, where, in addition, to the centrifugal force, the one-sided action of gravitation was also still operative, the shoots and roots took a definite middle position; the shoots and roots still grew in opposite directions, but their line of growth was inclined to the plane of rotation, at an angle dependent upon the rotating velocity. The position thus assumed was evidently the result of the combined action of the centrifugal force and gravity, which was manifested in the directions taken by the plants according to their comparative strength and respective influence on growth. In this way it was positively ascertained that terrestrial gravitation determines the positions of plant organs in respect to the earth (75).

Later, it was also shown that not only the perpendicular direction of stems and primary roots, but also the oblique or horizontal direction taken by lateral branches, roots, and rhizomes, is due to a peculiar reaction towards the force of gravitation.

The property of plants to assume a definite position with respect to the direction of gravitation is termed GEOTROPISM. It is customary also, as in the case of heliotropism, to speak of positive and negative geotropism, diageotropism, and transverse geotropism, according to the position assumed by the plant or organ with respect to the centre of the earth. Still another form of geotropic irritability, lateral geotropism, renders possible the winding of stem-climbers.

Negative Geotropism.—All vertically upward growing organs, whether stems, leaves (*Liliiflorae*), flower-stalks, parts of flowers, or roots (such as the respiratory roots of Avicennias, Palms, etc.), are negatively geotropic. In case such negatively geotropic organs are forced out of their upright position, they assume it again if still capable of growth. As in heliotropism, GEOTROPIC CURVATURE RESULTS FROM THE INCREASED GROWTH OF ONE SIDE AND THE RETARDED GROWTH OF THE OPPOSITE SIDE; and the region of greatest growth is, in general, also that of the greatest curvature. In negatively geotropic organs, growth is accelerated on the side towards the earth; on the upper side it is retarded. In consequence of the unequal growth thus induced, the erection of the free-growing extremity is effected. After the upright position is again attained, the one-sided growth ceases and the organ continues to grow in an upward direction.

The process of negative geotropic movement is dependent: (1) upon the vigour of the existing growth; (2) upon the sensibility of the organ; (3) upon the fact that the stimulus of gravity works most energetically when the apex of the orthotropic organ is removed about 135° from its position of geotropic equilibrium; the more nearly the zone capable of curvature approaches this position, the stronger is the motory stimulus; (4) and, also, upon the fact that after a stimulus has ceased to act upon a plant, the induced stimulation continues to produce so-called AFTER EFFECTS, just as by a momentary stimulus of light an after-perception persists in the eye.

These considerations determine the actual course of the directive movement of geotropism, which, as will be seen from the adjoining figure (Fig. 203), does not consist merely of a simple, continuous curvature. The numbers 1-16 show, diagrammatically, different stages in the geotropic erection of a seedling growing in semi-darkness and placed in a horizontal position (No. 1). The growth in the stem of the seedling is strongest just below the cotyledons, and gradually decreases towards the base. The curvature begins accordingly close to the cotyledons, and proceeds gradually down the stem until it reaches the lower, no longer elongating, portions. Through the downward movement of the curvature, and partly also through the after-effect of the original stimulus, the apical extremity becomes bent out of the perpendicular (No. 7), and in this way a curvature in the opposite direction takes place. Thus, under the influence of the stimulus, the stem bends backwards and forwards, until, finally, the whole growing portion becomes erect and no longer subject to the one-sided action of the geotropic stimulus.

Positive Geotropism, on the other hand, is observable in tap-roots, in many aerial roots, and in the leaf-sheaths of the cotyledons of many monocotyledons which penetrate the earth during germination. All these organs, when placed in any other position, assume a straight downward direction and afterwards maintain it. Formerly, it was

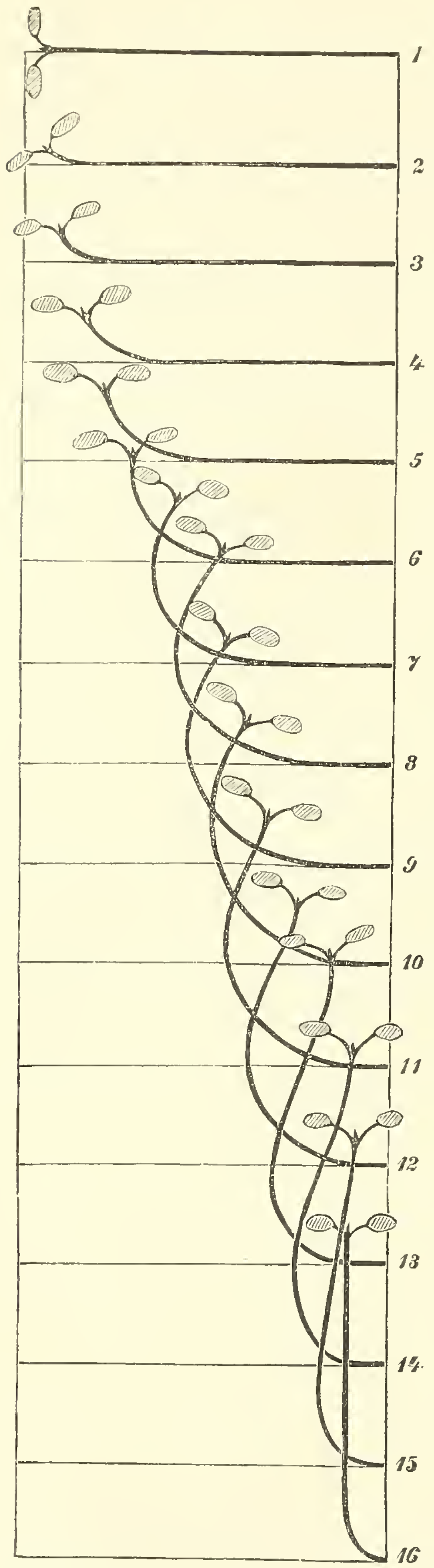


Fig. 203.—Different stages in the process of geotropic movement. The figures, 1-16, indicate successive stages in the geotropic curvature of a seedling grown in semi-darkness; at 1, placed horizontally; at 16, vertical. For description of intermediate stages see text (Diagrammatic.)

believed that this resulted solely from their weight and the pliancy of their tissues. It is now known that this is not the case, and that positive geotropic, like negatively geotropic movements, are possible only through growth. The power of a downward curving root-tip to penetrate mercury (specifically much the heavier), and to overcome the resistant pressure, much greater than its own weight, proves conclusively that positive heliotropism is a manifestation of a vital process. Positive geotropic curvature is due to the fact that THE GROWTH OF AN ORGAN IN LENGTH IS PROMOTED ON THE UPPER SIDE, AND RETARDED, EVEN MORE STRONGLY, ON THE SIDE TURNED TOWARDS THE EARTH. A young germinal root of *Castanea Vesca*, growing vertically, elongated equally on all sides 20 mm.; when placed horizontally, it exhibited a growth of 28 mm. on the upper and of only 9 mm. on the lower side. Fig. 204 illustrates the way in which the curvature takes place in the case of a root of the Broad Bean, which was marked at regular intervals with Indian ink and placed horizontally.

Diageotropism.—Most lateral branches and roots of the first order are diageotropic, while branches and roots of a higher order stand out from their parent organ in all directions. DIAGEOTROPIC ORGANS ARE ONLY IN A POSITION OF EQUILIBRIUM WHEN THEIR LONGITUDINAL AXES FORM A DEFINITE ANGLE WITH THE LINE OF THE ACTION OF GRAVITY. If forced from their normal inclination they return to it by curving. A special instance of diageotropism is exhibited by strictly horizontal organs, such as rhizomes and stolons, which show a strictly TRANSVERSE GEOTROPISM, and, if removed from their normal position, their growing tips always return to the horizontal. A more complex form of geotropic orientation is manifested by dorsiventral organs, *e.g.* foliage leaves, zygomorphic flowers. All such dorsiventral organs, just as radial organs that are diageotropic, form a definite angle with the direction of gravity, but are only in equilibrium when the dorsal side is uppermost. If, in spite of the proper inclination of the longitudinal axis, the dorsal side should lie underneath, it elongates until it comes back again into a dorsal position.

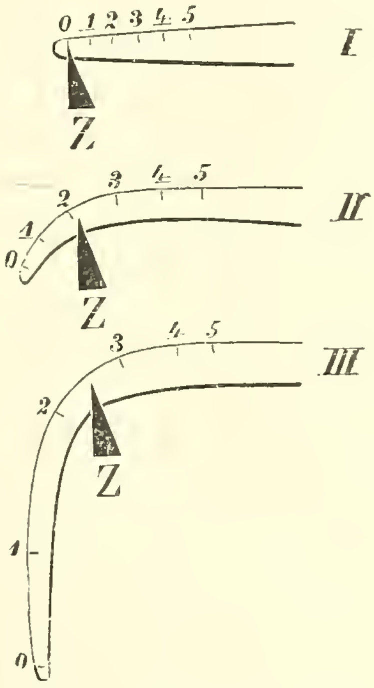


FIG. 204.—Geotropic curvature of the root of a seedling of *Vicia Faba*. *I*, Placed horizontally; *II*, after seven hours; *III*, after twenty-three hours; *Z*, a fixed index. (After SACHS.)

A state of torsion often results from the orientation movements of dorsiventral organs to recover from abnormal positions. Similarly, a torsion must also, of necessity, occur when a geotropic organ, which has become curved over toward its parent axis, turns itself about so as to face outwards (EXOTROPISM). The rotation of the ovaries of many *Orchidaceae*, of the flowers of the *Lobeliaceae*, of the leaf-stalks on all hanging or oblique branches, of the originally reversed leaves (with the palisade parenchyma on the under side) of the *Alstroemeriae*, and of *Allium ursinum*, all afford familiar examples of torsion regularly occurring in the process of orientation (76).

Stem-Climbers.—In addition to the better-known forms of geotropism already mentioned, stem-climbers exhibit a peculiar and only recently recognised geotropic movement, by means of which they are enabled to twine about upright supports. This movement depends upon the geotropic promotion of the growth of one side (not, as in negative or positive geotropism, of the upper or lower portions). Thus a geotropic curvature in a horizontal plane is produced (LATERAL GEOTROPISM), resulting in a revolving motion of the shoot apex. Stem-climbers occur in very different plant families; and although an upward growth is essential to their full development, which they do not attain if left on the ground, their stems are not able of themselves to maintain an erect position. The erect stems of other plants, which often secure their own rigidity only through great expenditure of assimilated material, are made use of by stem-climbers as supports, on which to spread out their assimilatory organs in the free air and light. The utilisation of a support produced by the assimilatory activity of other plants is a peculiarity they possess in common with other climbers, such as tendril- and root-climbers. Unlike them, however, the stem-climbers accomplish their purpose, not through the use of lateral clinging organs, but by the capacity of their main stems to twine about a support. The first internodes of young stem-climbers, as a rule, stand erect. By further growth the free end curves energetically to one side, and assumes a diageotropic, more or less oblique or horizontal position. At the same time the inclined apex begins to revolve in a circle either to the right or to the left. This is the movement which it has been customary to speak of as "revolving nutation," but which it is better to term REVOLVING MOVEMENT. The expression "nutation" is not in this case correct, as by it are understood autonomic movements; while THE REVOLVING MOVEMENTS OF STEM-CLIMBERS RESULT FROM THE EXTERNAL SIMULUS OF GEOTROPISM, which causes a promotion of growth in either the right or left side of the young internodes of the inclined shoot apex. As a result of this, a movement towards the other side is induced. On account of the direct connection of the apex of the shoot with the lower erect internodes, this revolving movement necessarily gives rise to a similar rotation of the revolving apex on its longitudinal axis. Through this rotation the torsion, which would otherwise be produced by the revolving movement of the inclined tip of the shoot, is released. (This process will at once become apparent by imitating the movement with a rubber tube.) Thus the apex of a stem-climber sweeps round in a circle like the hand of a watch, and rotates at the same time like the axle to which the hand is attached. Through this rotation of the shoot apex, the part of the stem subjected to the action of the lateral geotropism is constantly changing; and the revolving movement once begun, must continue, as no position of equilibrium can be attained.

Without the constant and unchanging action of gravitation in determining the direction of the revolving movement, the twining of a shoot continuously about a support is hardly conceivable. It is accordingly not without reason that the revolving movement is a continuous, fixed, geotropic movement, and not an autonomic nutation without definite directive force. Lateral geotropism is a physiological requisite for the climbing, and the existence of stem-climbers as such is dependent upon this peculiar form of geotropism (77). To this dependence, however, is also due the fact that stem-climbers can only twine about upright or slightly inclined supports. This is, it is true, a limitation to their power of climbing, but one which is not without advantage, for the plants are thus constrained to ascend to freer light and air.

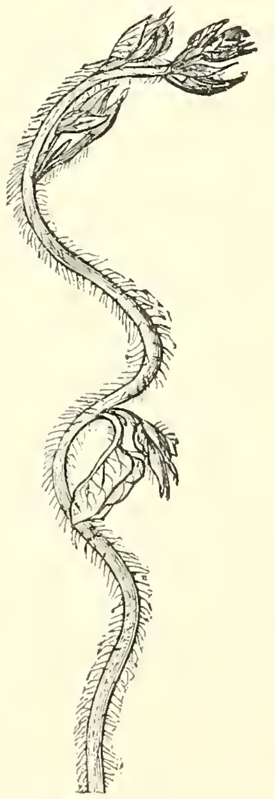


Fig. 205.—Free coils formed by a shoot of *Ipomoea purpurea*. (From Detmer's *Physiol. Pract.*)

When an upright support occurs anywhere in the immediate neighbourhood of the apex of a climbing shoot it is sure to be discovered. The apical extremity, the movement of which is but little disturbed by the leaves, which remain for a long time undeveloped, is forced by its lateral geotropism against the support, and by its next revolutions twines around it. If the support be thin, the coils, at first almost horizontal, are only loosely wound about it. Later they become more spiral, and so wind more tightly. This is accomplished by the ultimate predominance of negative geotropism in the coiled portions of the stem, which tends continually to draw out the coils and make the stems upright. This action of negative geotropism is well shown in the case of shoots which have formed free coils without a support (Fig. 205). By the resistance offered by the supports to the complete elongation of the spiral stems, the shoots are held firmly in position. In many twining plants the roughness of their surfaces (due to hairs, bristles, hooks, furrows) also assists in preventing the shoots sliding down their supports. The autonomic torsion arising in the older portions of the stems is also of assistance in holding climbing plants, especially those with furrowed stems, tightly wound about their supports. The twining of stem-climbers, as well as the attachment to their supports, is thus due to geotropic processes of growth, and not, as in tendril-climbers, to contact stimuli.

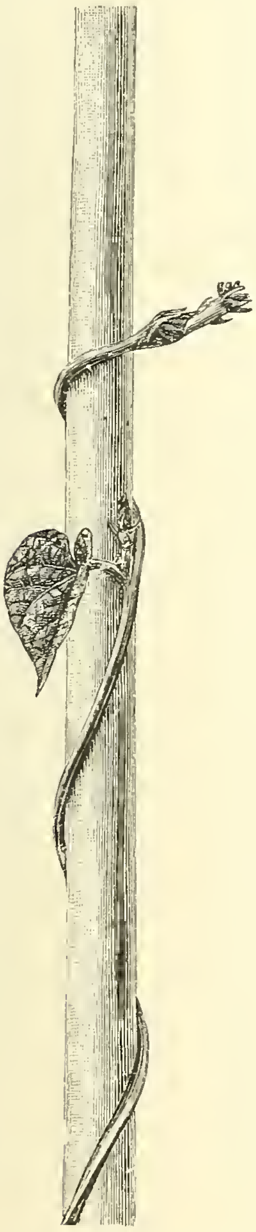


FIG. 206.—A sinistrorse stem-climber, *Pharbitis hispida.* The upper leaves remain small for a long time.

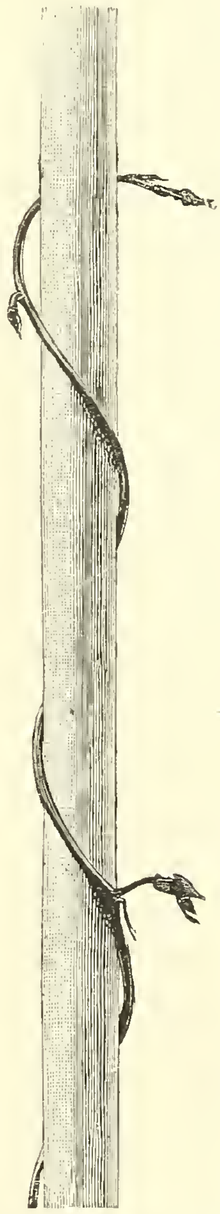


FIG. 207.—A dextrorse stem-climber, *Myrsiphyllum asparagoides.* The short lateral shoots have developed phyllocladia.

In addition to the autonomic torsions, a torsion from purely mechanical causes is necessarily manifested in the elongation of the coils of a twining stem which are at first nearly horizontal, so far at least as it is not equalised by the free movement of the apex.

The direction of the revolving movements, and accordingly also of the windings, of most stem-climbers is constant. The twining stems are for the most part SINISTRORSE (*Convolvulus, Phaseolus, Pharbitis,* etc.). Seen from above, the windings run from the north towards the west; that is just the reverse of the movement of the hands of a watch. Viewed from the side, the windings ascend the support from the left below to the right above (Fig. 206). DEXTRORSE stem-climbers with windings from east to west occur less frequently (Hop, Honeysuckle, *Polygonum Convolvulus*, etc.). In the example chosen for illustration (*Myrsiphyllum asparagoides*, Fig. 207) the undeveloped condition of the lateral members in comparison with the elongated internodes of the stem is very apparent. A very few plants, such as *Blumenbachia lateritia*, *Hibbertia dentata*, and *Scyphantus*, seem able to climb equally well either to the right or to the left. A similar irregularity is shown in *Solanum Dulcamara*, which, however, rarely winds, and then only under special circumstances.

When the apex of a sinistrorse shoot points towards the north, it is the east side of which the growth is promoted by geotropism; in dextrorse climbers, on the contrary, the growth of the west side is more rapid. From the fact that the promotion of growth occurs always on the same side, it will be apparent that the apex of an inverted twining stem must unwind from its support. (Concerning the behaviour of stem-climbers on the Klinostat compare p. 263) (^{78}).

Curvature of Grass-Haulms.—All the examples of geotropic movements, so far observed, took place in the growing portions of plants, and, whether occurring in unicellular or multicellular organs, were due to a disturbance of the course of growth. A curvature even of lignified twigs can also be produced by the one-sided stronger growth of the cambium and of the young secondary tissues. Even many-year-old branches of Conifers are all able, although slowly, to exhibit geotropic curvatures (^{79}). THE NODES OF GRASSES SHOW THAT RESTING TISSUES ALSO CAN BE EXCITED TO NEW GROWTH BY THE STIMULUS OF GRAVITATION. The knot-like swellings on the haulms of the Grasses are not nodes in a morphological sense, but are cushion-like thickenings of the leaf-sheaths above their actual insertion on the shoot axis. The part of the stem thus enveloped is very tender and flexible. When a grass-haulm is laid horizontally, which not unfrequently occurs through the action of the wind or rain, the nodes will begin to exhibit an energetic growth on their lower sides. As the upper sides of the nodes take no part in the growth, but are instead frequently shortened through pressure and

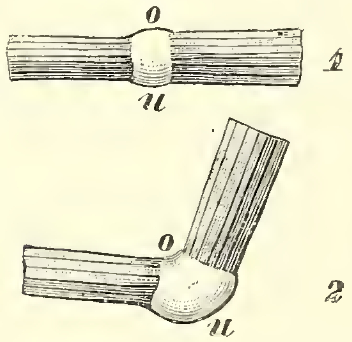


Fig. 208.—Geotropic erection of a grass-haulm by the curvature of a node. 1, Placed horizontally, both sides (*u*, *o*) of the node being of equal length; 2, the under side (*u*) lengthened, the upper side (*o*) somewhat shortened; as a result of the curvature the grass-haulm has been raised through an angle of 75°.

loss of water, knee-like curvatures are formed at the nodes, by means of which the haulm is again quickly brought to an erect position (Fig. 208).

Modifications in the character of the geotropism, as of the heliotropism, of an organ may be occasioned by the operation of internal as well as external influences. Such changes in their geotropic position frequently occur, as VÖCHTING has demonstrated, during the development of flower-buds, flowers, and fruits (buds and flowers of *Papaver*, flowers and fruits of *Aquilegia*, *Delphinium*, *Aconitum*, and in the burial of the fruit of *Trifolium subterraneum*, *Arachis hypogaea*, etc.). Of the changes in the geotropic conditions of plant organs due to external causes, those are particularly noticeable which result from a failure of a sufficient supply of oxygen, by which, for example, roots and rhizomes are made negatively geotropic. And even more important are the modifications arising from the action of light, by which the geotropic irritability of rhizomes and foliage leaves may be so modified or weakened as to permit of more advantageous heliotropic positions.

C. *Hydrotropism*, *Caloritropism*, *Thermotropism*, *etc.*

Whenever any external force or substance is important to the vital activity of a plant or any of its organs, there will also be found to be developed a corresponding irritability to their influences. Roots in dry soil are diverted to more favourable positions by the presence of greater quantities of moisture. The force of this POSITIVE HYDROTROPISM may be so great as to overcome the geotropic equilibrium of the roots, and thus give rise to hydrotropic curvatures. Conversely, the sporophores of many mould Fungi avoid moisture. To this property is due the fact, so advantageous for the distribution of the spores, that their sporangiophores grow directly away from a moist substratum. Corresponding to the chemotactic irritability of Bacteria and spermatozoids, roots, fungus hyphae, and pollen tubes exhibit positive and negative CHEMOTROPIC CURVATURES. These vary according to the concentration of the solution, so that an attractive substance, at a higher concentration, may act repulsively. THERMOTROPISM (due to the stimulus of heat), RHEOTROPISM (occasioned by the direction of water currents), and AEROTROPISM, a form of chemotropism, are additional phenomena, which have been distinguished as arising from the special action of external stimuli, and which stand in direct relations to certain vital requirements of plants (80).

In the case of ELECTROPISM, which has also been demonstrated in plants, no such essential relations have been discovered; the disposition of plant organs in a direction contrary to that of an electric current seems in no way to affect their growth. The fact of the existence of electropism in plants shows clearly that an irritability may be present, from which no direct benefit is ordinarily derived, and which accordingly could not have been attained by natural selection.

D. *The Method of Slow Rotation—The Klinostat*

All the curvatures of growth previously discussed have been induced by the one-sided action of stimuli, the source of which determined the direction of the movements as well as the position of equilibrium. An influence operating equally on all sides is unable to produce a curvature in an organ of which the irritability is equally developed on all sides. In like manner no curvatures can take place when the plant is uniformly rotated, with a velocity sufficient to preclude the continuous operation of a stimulus on any one point long enough to occasion a one-sided growth. As in that case, no one side will be exclusively acted upon, but the growth of all will be equally promoted or retarded; the action of external influences, although exerted in only one direction, will be equalised. On this account the "method of slow rotation," originally instituted by SACHS, is of great assistance in the observation and investigation of the phenomena of movements. By means of it, heliotropic movements due to one-sided illumination may be prevented without the necessity for either exposing the plants to the injurious effects of continued darkness, or providing for an equal illumination on all sides. This method is, moreover, of especial value in investigating the movements due to the action of gravitation, for it is not possible to exclude its influence, as it is those arising from light, definite temperature, oxygen, etc.

WHEN PLANTS ARE SLOWLY ROTATED ON A HORIZONTAL AXIS, THE ONE-SIDED ACTION OF GRAVITATION IS ELIMINATED AND GEOTROPIC CURVATURE IS THUS PREVENTED in organs which react equally on all sides. The rotations are best produced by the KLINOSTAT, an instrument by means of which an exactly horizontal axis is rotated by clock-work ([81]). That geotropic curvatures of radial organs are, in fact, precluded by means of the klinostat, furnishes a remarkable corroboration of the result of KNIGHT'S experiments, and may also be regarded as a further proof that such curvatures are due to terrestrial gravitation. Through the equalisation of the action of external directive influences, radial portions of plants exhibit on the klinostat only such movements as arise from internal causes. The most important of these autonomic movements are those resulting in epinastic and hyponastic curvatures (p. 248), and the retrogression of recently formed paratonic curvatures through longitudinal extension (autotropism).

Such autonomic movements should not be confused with those exhibited by dorsiventral organs on the klinostat, in consequence of the unequal irritability of their different sides. Through the special irritability of the dorsal side of foliage leaves and zygomorphic flowers, it is during their rotation more strongly acted upon by geotropic influence than the ventral side; as a result of this curvatures are produced which so closely resemble those resulting from epinasty that they were for a long time actually considered as such. When stem-climbers are rotated on the klinostat, their revolving movement ceases, the part of the stem capable of growth unwinds and straightens, and afterwards exhibits only irregular nutations.

E. *Curvatures induced by Contact Stimuli*

The protoplasm of plants, like that of animals, exhibits an irritability to contact, whether momentary or continuous. This is apparent, not only from the behaviour of the naked protoplasmic bodies of spermatozoids, swarm-spores, plasmodia, and amœbæ, but also from the reactions manifested by walled cells and by whole organs, the functions of which may be so disturbed by the action of mechanical stimuli that death ensues.

The almost universal irritability of vegetable protoplasm to mechanical stimulation is utilised by a number of plants for the production of movements which lead to their ultimate attachment to the irritating body. Tendril-climbers, in particular, have developed this irritability to contact stimuli as a means of attaching themselves to supports (cf. p. 66, Fig. 69); and in that way are enabled to elevate their assimilating and also their reproductive organs into more favourable situations. In the case of twining plants which possess similar powers of climbing, the process of elevation, as has already been shown, is accomplished by means of the geotropic irritability of the stems themselves. In the case of tendril-climbers, on the contrary, the attachment to the support is effected, not by the main axis of the plant, but by lateral organs of different morphological character. These may either maintain, at the same time, their normal character and functions, or, as is usually the case, become modified and as typical tendrils serve solely as climbing organs. From the researches of C. DARWIN and MACDOUGAL it appears that contact with the support causes the cells of the touched side to shorten elastically owing to loss of water, while the growth of those on the opposite side continues ([82]). As a result of this, a sharp curvature of the tendril ensues, which coils it about the support. The more slender the tendrils and the stronger their growth, the more easily and quickly this process occurs. Through the tendency of the curvature to press the tendrils more and more firmly against the support, deep impressions are often made by them upon yielding bodies, soft stems, rubber tubing, etc.

In the more typically developed tendrils the curvature does not remain restricted to the portions directly subjected to the action of the contact stimulus. Apart from the fact that, in the act of coiling, new portions of the tendrils are being continually brought into contact with the support and so acted upon by the stimulus, the stimulation to curvature is also transferred to the portions of the tendril not in contact with the support. Through the action of the propagated stimulus, not only is the free apex of the tendril turned more quickly around the support, but a tendency to curvature is imparted to the portion of the tendril between the support and the parent shoot. As it extends between two fixed points, this tendency causes it to coil spirally, like a corkscrew. With the spiral coiling, a torsion is produced, and since, on account of the fixed position of the two end points, it cannot be exerted in one direction only, the spiral, for purely mechanical reasons, coils partly to the left and partly to the right. POINTS OF REVERSAL (x) thus occur in the windings which, in equal numbers to the right and to the left, equalise the torsion (Fig. 209). Through the spiral coiling of the tendrils the parent-stem is not only drawn closer to the support, but the tendrils themselves, through their consequent elasticity, are enabled to withstand the injurious effects of a sudden shock.

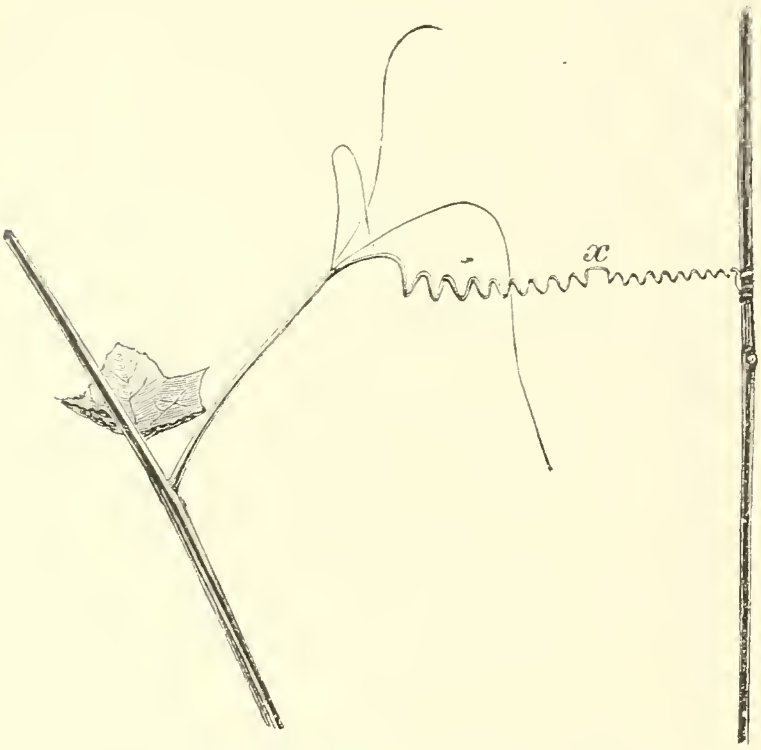


FIG. 209.—Portion of a stem of *Sicyos angulatus* with tendril ; x, point of reversal.

Advantageous changes also take place in the anatomical structure of the tendrils after they are fastened to the supports. The young tendrils, after their elongation, exhibit active nutations, and thus the probability of their finding a support is enhanced. During this time they remain soft and flexible, while the turgor rigidity of their apices is maintained only by collenchyma. In this condition they are easily ruptured, and have but little sustaining capacity. As soon, however, as a support is grasped, the coiled-up portion of the tendrils thickens and hardens, while the other part lignifies, and becomes so strengthened by sclerenchymatous formations that the tendrils can finally sustain a strain of many pounds. When the tendrils do not find a support they usually dry up and fall off, but in some cases they first coil themselves into a spiral.

The tendrils of many plants (*Cobaea*, *Cissus*) are irritable on all sides ; others, on the contrary, on only the lower side (tendrils of *Cucurbitaceae* and others with hooked tips) ; while others possess extremely sensitive flanks (*Mutisia*). In some cases the tendrils quickly coil themselves to the support (*Passiflora*, *Sicyos*, *Bryonia*) ; while in other tendrils the supports are very slowly grasped (*Smilax*, *Vitis*).

According to PFEFFER'S investigations, it is of great importance to the tendrils in the performance of their functions that they are not induced to coil by every touch, but only through CONTACT WITH THE UNEVEN SURFACE OF SOLID BODIES (as thus adjacent cells become unequally affected). Rain-drops consequently never act as a contact stimulus; and even the shock of a continued fall of mercury produces no stimulation (83). Tendril-climbers are not, like twining plants, restricted to nearly vertical supports, although, on account of the manner in which the tendrils coil, they can grasp only slender supports. A few tendril-climbers are even able to attach themselves to smooth walls. Their tendrils are then negatively heliotropic, and provided at their apices with small cushion-like outgrowths, which may either develop independently on the young tendrils, or are first called forth by contact irritation. Through their sticky excretions these cushions become fastened to the wall and then grow into disc-like suckers, the cells of which come into such close contact with the supporting wall that it is easier to break the lignified tendrils than to separate the hold-fasts from the wall. Fig. 210 represents the tendrils of *Ampelopsis Veitchii* (*Vitis inconstans*). The suckers occur on its young tendrils in the form of knots. In *Ampelopsis hederacea* the suckers are only produced as the result of contact, and the tendrils of this plant require thin supports.

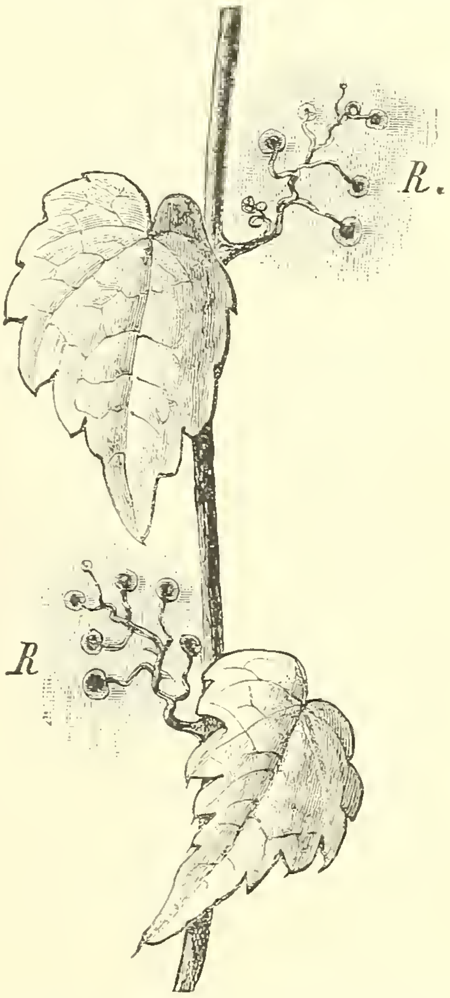


FIG. 210.—Portion of a climbing shoot of *Ampelopsis Veitchii* (*Vitis inconstans*). The tendrils (*R*) have fastened themselves to a smooth wall by means of hold-fasts.

Sometimes, as in the case of *Lophospermum scandens* (Fig. 211), the leaf-stalks, although bearing normal leaf-blades, become irritable to contact stimuli and function as tendrils. Of leaf-stalks which thus act as tendrils, good examples are afforded by *Tropaeolum*, *Maurandia*, *Solanum jasminoides*, *Nepenthes*, etc. The subsequent modifications occurring in more perfectly developed tendrils are not noticeable in the case of petiolar tendrils, although the coiling portion of the leaf-stalks of *Solanum jasminoides* do become strongly thickened and lignified; while the leaf-blades of *Clematis*, by remaining small for a time, enhance the tendril-like character of their leaf-stalks, and by bending backwards also assist in maintaining the initial contact with a support. At other times the midribs of the leaf-blades themselves become prolonged, and assume the function of tendrils (*Gloriosa*, *Littonia*, *Flagellaria*). In many species of *Fumaria* and *Corydalis*, in addition to the leaf-stalks, even the leaf-blades of the leaflets twine around slender supports, while the parasitic shoots of *Cuscuta* (Fig. 186) are adapted for both twining and climbing. Climbing parts of the thallus occur in some Thallophyta (Florideae) ([84]).

F. *Curvatures of Growth due to Variations in Light and Temperature*

The flowers and foliage leaves of many plants exhibit the peculiarity that their different sides (the upper and under sides of foliage-leaves and leaf-stalks, the inner and outer sides of floral leaves) show an unequal growth in response to even transitory and slight variations in temperature and in the intensity of light. Whenever, on account of such variations, the growth of the under side of a leaf exceeds that of the upper side, the whole leaf moves upwards and towards the parent axis; while if the growth of the upper side is the stronger, the leaf is depressed.

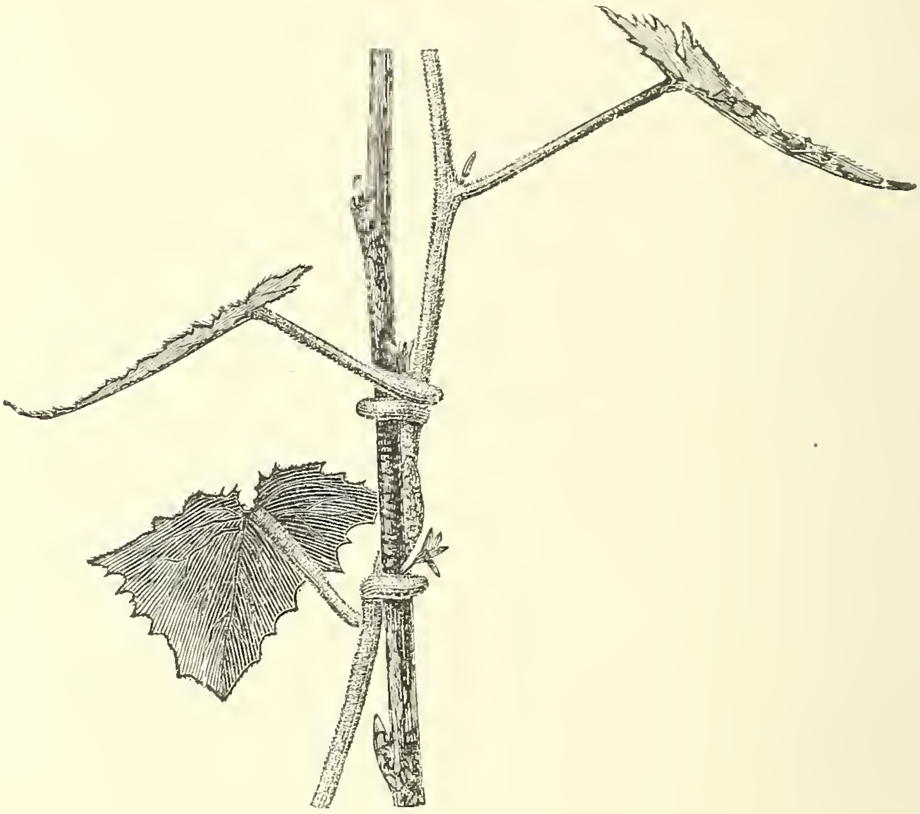


FIG. 211.—*Lophospermum scandens* climbing by means of its tendril-like petioles.

Movements of this nature are especially noticeable in flower-leaves, and bring about the opening and closing of the flower. A rise of temperature causes the flowers of the Tulip and Crocus, and also those of *Adonis*, *Ornithogalum*, and *Colchicum*, to open, while sudden cooling causes them to close. Tulips and Crocuses, if brought, while still closed, into a warm room, open in a very short time; with a difference of temperature of 15°-20° C., in from two to four minutes. Crocuses respond to an alteration in temperature of $\frac{1}{2}$° C.; Tulips to a variation of 2°-3° C. In warm sunshine the spring or summer flowers are open for the visits of insects, but on a lowering of temperature the sexual organs are covered up and protected. The stronger growth of one side occurs in this case either at the base or upper part of the perianth leaves.

The flower-heads of *Taraxacum*, *Leontodon*, and other Composites, also the flowers of *Nymphaea*, *Cacti*, etc., open when illuminated, and close when kept in darkness (Fig. 212).

Variation of light produces also unequal growth in foliage-leaves, particularly in those of the *Chenopodiaceae*, *Caryophyllaceae*, and *Balsaminaceae*, and cause them to assume so-called SLEEP POSITIONS.

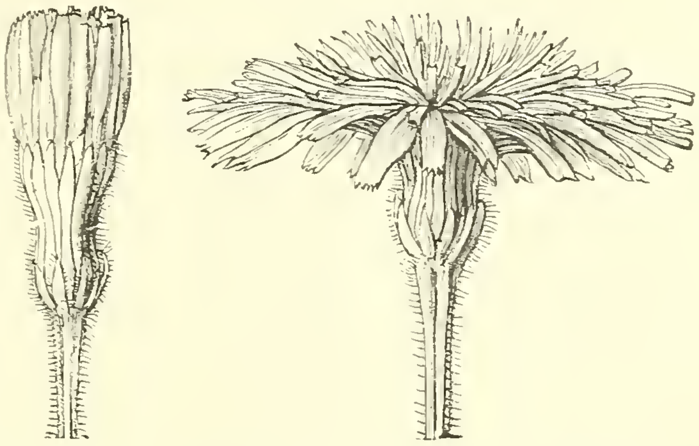


FIG. 212.—Flower-head of *Leontodon hastilis*, closed when kept in darkness, open when illuminated. (From DETMER'S *Physiol. Pract.*)

In many instances the movements of the floral leaves are produced by variations of light as well as of temperature: for example, the flowers of the Tulip and Crocus open in the light and close in the dark, although the temperature remains constant. In the case of opposing external influences, the resulting direction of the movement of the flower-leaves is determined by the one which is predominant. The dependence of these movements upon different, and often opposing, influences, together with the continuance of movements induced by previously operative influences, was for a long time a difficult problem, and obscured the discovery of their true cause (85).

These movements, occasioned by variations in the illumination and temperature, must not be confused with those of heliotropism and thermotropism; in both of which the movement induced in an organ is dependent upon its relative position with respect to the source of the light or heat, and not upon the varying intensity of the stimulus.

3. Movements due to Changes of Turgor (Movements of Irritability)

The various movements hitherto considered are, to a large extent, the result of the action of forces acting on growth. These movements were therefore confined to organs, or parts of organs, still in a state of growth. In contrast to the almost universal immobility of all fully-grown organs, it is particularly interesting to find that some plants have found a means of carrying on vigorous movements without the assistance of growth.

It has already been shown (p. 164) that through the pressure of increasing turgidity the elastic cell walls become greatly distended and the cell cavity largely expanded, while, on the other hand, the cell walls shrink and the cell becomes smaller when the turgor is diminished (Fig. 168). It is to these changes in volume, which thus result from alterations in turgor, that the varying movements of fully developed living organs are due.

Such variation movements occur only in leaves (foliage and flower leaves). These movements are especially noticeable in the compound leaves of the *Leguminosae* and *Oxalideae*, and also in the leaflets of *Marsilia* (a water-fern). In the motile regions of these leaves special masses of tissue are, both physiologically and anatomically, adapted for the promotion of this form of movement.

This tissue appears externally as a firm cushion or PULVINUS, sharply distinguished from the rest of the leaf-stalk, and is the direct cause of the leaf movements. Anatomically considered, the pulvinus consists, for the most part, of strongly turgescent parenchyma with very elastic cell walls. The vascular bundles and mechanical elements, which, in other portions of the leaf-stalk, have an approximately circular arrangement, unite in the pulvinus in the form of a single flexible strand, and so offer little opposition to the movement of the leaf resulting from the curvature of the motile region (cf. Fig. 169, *i*). The parenchyma of the pulvinus forms a thick enveloping layer about this axial strand, by means of which, through the pressure arising from a difference in the turgescence of its opposite sides, a movement of the whole leaf-blade is brought about, similar to that of the outspread hand by the motion of the wrist.

These variation movements are either autonomic, when the variations of turgor are due to no recognisable external influence, or paratonic, when the turgor is regulated in a definite way by the action of external stimuli.

Autonomic Variation Movements.—A remarkable example of this form of movement is furnished by the small lateral leaflets of *Desmodium* (*Hedysarum*) *gyrans*, a papilionaceous plant growing in the damp Ganges plains. In a moist, warm atmosphere (22°-25°) these leaflets make circling movements which are in no way disturbed by variations in the intensity of the light, and which are of such rapidity that their tips describe a complete circle in 1-3 minutes. The autonomic variation movements of *Trifolium* and *Oxalis* take place, on the contrary, only in darkness. Thus the terminal leaflets of *Trifolium pratense* exhibit oscillatory movements in the dark with an amplitude which may exceed 120°, and are regularly repeated in periods of 2-4 hours; but on exposure to light the leaflets cease their oscillations and assume a fixed light position.

Paratonic Variation Movements are chiefly induced by variation in the intensity of the light, by the stimulus of gravitation, and by mechanical irritation (shock, friction), and also, but more rarely, by variations of temperature. The pulvini of leaves may be affected by several different stimuli; the leaves of *Mimosa pudica*, for example, are set in motion by the action of light, and also by the stimulus of a shock, and in addition exhibit autonomic movements.

A change from light to darkness, as from day to night, occasions NYCTITROPIC MOVEMENTS, or the so-called SLEEP MOVEMENTS. In the day or light position, which is the same as that of diaheliotropic foliage-leaves, the leaf-blades are perpendicular to the incident rays of light. With the commencement of darkness the leaves or the single leaflets fold either upwards with their upper surfaces inward, or downwards with their lower surfaces together, and so remain until the diurnal position is again assumed on recurring illumination. THE VARIATIONS IN TURGESCENCE IN THE OPPOSED HALVES OF THE JOINT STAND IN INVERSE RELATION TO ONE ANOTHER; AN INCREASE IN TURGESCENCE IN THE LOWER HALF CORRESPONDS TO A DIMINUTION IN THE UPPER PORTION, AND INVERSELY (86).

In the peculiarly constructed pulvini of the Marantaceae the side, which becomes concave, shortens, according to DEBSKI, by deformation of its cells, as a result of increase of turgescence.

As sleep movements are also manifested by plants growing in tropical climates, where no injurious nocturnal fall of temperature occurs, the purpose of the sleep position suggested by DARWIN, viz. the protection of the leaves from excessive cooling, does not hold in all cases. STAHL seeks it also in the lessening of the formation of dew, and the more energetic transpiration of the unwetted leaves which would result.

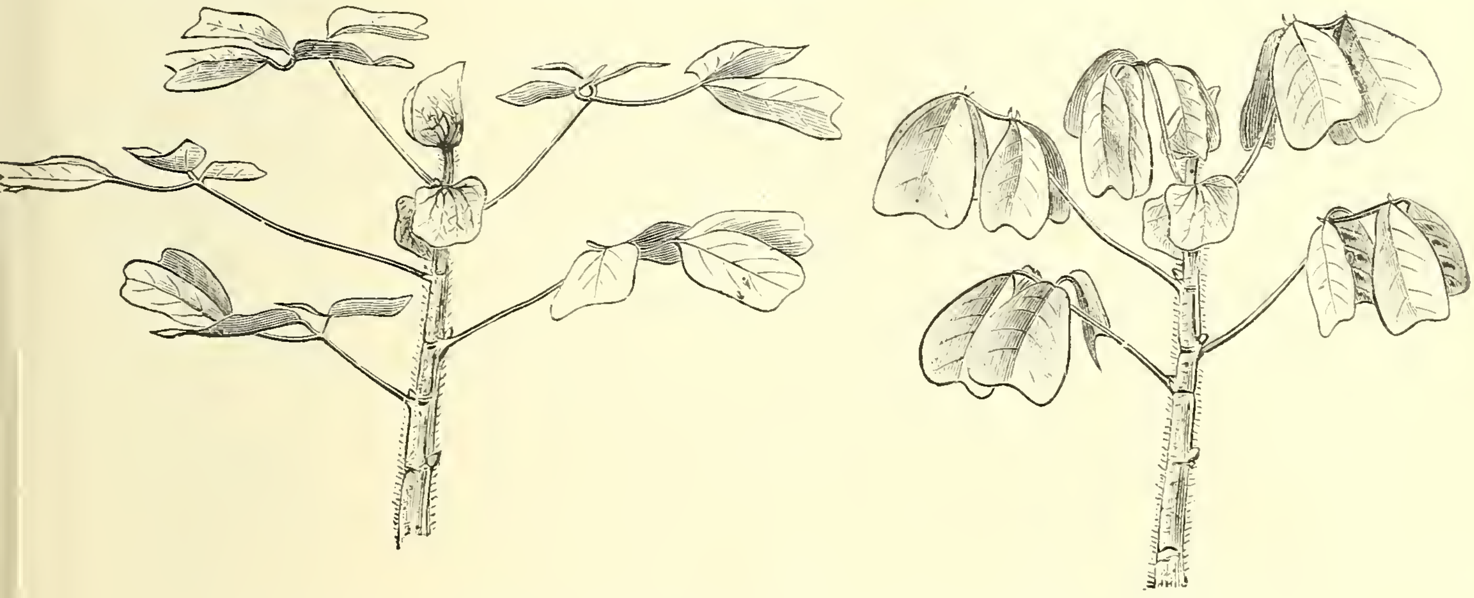


FIG. 213.—*Amicia zygomeris*, showing diurnal and nocturnal position of leaves.

Sleep movements are particularly noticeable in *Phaseolus*, *Trifolium*, *Robinia*, *Acacia lophantha*, *Amicia zygomeris* (Fig. 213), *Mimosa pudica*, etc.

Too intense light frequently causes the change from the diurnal position, and a movement either towards or away from the nocturnal position. The leaflets of the common Locust (*Robinia pseudacacia*) are folded downwards at night. In ordinary diffuse daylight they assume their diurnal, outspread position; but, if exposed to the direct rays of the mid-day sun, they turn obliquely upwards. In many plants ALTERATIONS IN THE INTENSITY OF THE LIGHT CHANGE THE GEOTROPISM OF THE MOTILE ORGANS; the sleep movements are then accomplished by the help of geotropic variation movements (*Phaseolus*, *Lupinus*) (87).

The change from the diurnal to the nocturnal position continues for a time to take place, even in constant darkness or prolonged illumination. The leaves themselves seem to have a tendency to pass at regular intervals from one condition to the other (p. 237). The daily periods are the result of the stimulus imparted by the light, the periodic action of which induces the regular changes of position. If, however, the external stimulus ceases to operate, the internal disposition still continues for some time to give rise to visible after-effects, until finally, from the abnormal conditions, an abnormal state of rigor (light rigor, dark rigor) and symptoms of disease are manifested (88).

Only a few plants respond with pronounced variation movements to mechanical irritation (shock, friction, injury). Formerly, these alone were considered irritable plants, as in the vegetable kingdom only the apparent mechanical irritations, from which visible movements resulted, were then regarded as stimuli (on organs to receive mechanical stimuli cf. pp. 66 and 263).

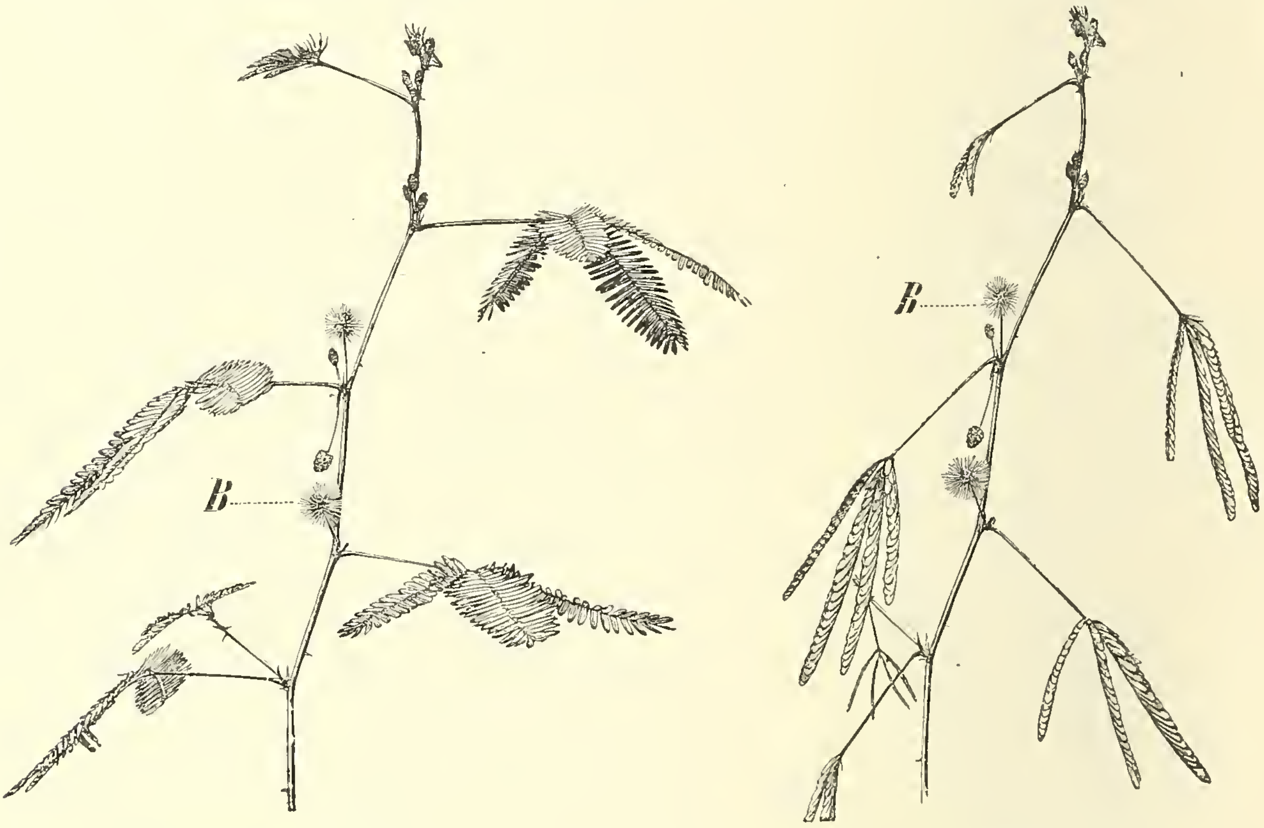


FIG. 214.—*Mimosa pudica*, with leaves in normal, diurnal position ; to the right, in the position assumed on stimulation ; *B*, flowers.

Of irritable plants in this sense, mention has already been made of *Dionaea muscipula* (p. 215), whose leaves, when touched on the upper side, especially if the bristles are disturbed, fold together. The most familiar example of this irritability to mechanical stimuli is furnished by *Mimosa pudica*, a tropical leguminous shrubby plant, which owes its name of sensitive plant to its extreme sensitiveness to contact. The leaves of this plant are doubly compound (Fig. 214). The four secondary leaf-stalks, to which thickly-crowded leaflets are attached left and right, are articulated by well-developed pulvini with the primary leaf-stalks ; while they, in turn, as well as the leaflets, are similarly provided with motile organs. Thus all these different parts are capable of independent movement, and the appearance of the entire leaf becomes, in consequence, greatly modified. In their unirritated, light position (Fig. 214, on the left) the leaf-stalk is directed obliquely upwards, while the secondary petioles with their leaflets are extended almost in one plane. Upon any vibration of the leaf, in favourable conditions of temperature (25°-30° C.) and moisture, all its parts perform rapid movements. The leaflets fold together, and, at the same time, move forward, the secondary petioles lay themselves laterally together, while the primary leaf-stalk sinks downwards (Fig. 214, on the right). Leaves thus affected, if left undisturbed, soon resume their former position.

The behaviour of the leaves is still more marvellous when only a few of the leaflets are acted upon by the stimulus. This is easily demonstrated by holding a burning match near the leaflets of one of the pinnæ. The leaflets directly affected by the flame fold quickly upwards, and this movement is performed successively by each pair of leaflets of the pinna until the articulation with the primary leaf-stalk is reached. The stimulation is then conveyed to the other pinnæ, the leaflets of which go through the same movement in a reverse order; finally, the secondary petioles themselves draw together. Suddenly, when the whole process seems apparently finished, the main leaf-stalk in turn makes a downward movement. From this leaf the stimulus is able to travel still further through the stem, and it may thus induce movement in leaves 50 cm. distant.

The movements of the pulvini are due solely to differences in turgidity which, as in the case of nyctitropic movements, occur antagonistically in the halves of the pulvinus. It has been observed that a sudden escape of water into the intercellular spaces takes place out of the cells of the lower or irritable side of the pulvinus of the primary leaf-stalk. According to the recent investigations of HABERLANDT, the conduction of the stimulus does not appear to be accomplished by the movement of the water thus discharged, but by the mucilaginous contents of sacs which are situated in the phloem portion of the vascular bundles. MACDOUGAL was, however, unable to induce the movements by causing differences in the hydrostatic pressure. The position of an irritated leaf resembles externally its sleep or nocturnal position, but in reality the turgor tension of the pulvinate motory organ is different.

Robinia, *Oxalis acetosella*, and *Biophytum* (*Oxalideae*) exhibit similar, although less active, movements, under the influence of mechanical stimuli.

The state of rigor sometimes occurring in motile organs may also be best observed in *Mimosa*, for, although so sensitive to the action of external influences, it does not exhibit its irritable movements at all times. Whenever the temperature of the surrounding air falls below a certain degree, no movements take place, and the whole plant passes into a condition known as COLD RIGOR, while, on the other hand, at a temperature of about 40°, heat rigor occurs. Drought rigor is induced, just before withering, by an insufficient supply of water, and a dark rigor by a prolonged retention in darkness. In a vacuum, or on exposure to hydrogen and other gases—chloroform vapour, etc.—movement also ceases, partly on account of insufficient oxygen, and partly from the actual poisonous action of the gases themselves. If the state of rigor is not continued too long, the original irritability will again return on the restoration of normal conditions (89).

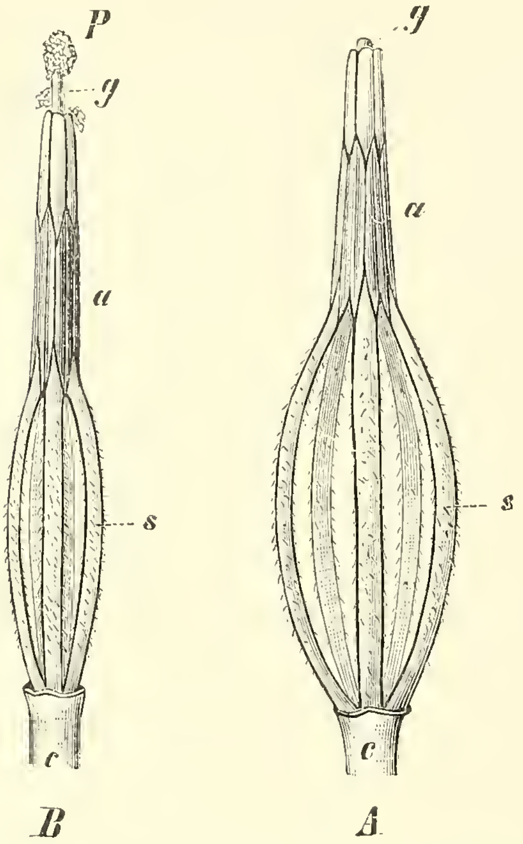


Fig. 215.—A single flower of *Centaurea jacea* with perianth removed: *A*, stamens in normal position; *B*, stamens contracted; *c*, lower part of tubular perianth; *s*, stamens; *a*, anther-tube; *g*, style; *P*, pollen. (After Pfeffer, enlarged.)

The movements of irritability exhibited by the staminal leaves of some *Berberidaceae* (*Berberis*, *Mahonia*) and *Compositae* (*Cynareae* and *Liguliflorae*) bear a certain relation to those of foliage leaves. The bow-shaped filaments of the stamens of the *Compositae* straighten upon mechanical irritation. As they frequently contract 10-20 per cent of their length, the style becomes extended beyond the anther-tube (Fig. 215). The reduction in the length of the filaments is accompanied by a moderate increase in their thickness, due to the elastic contraction of the cell walls, and the consequent expulsion of water into the intercellular spaces (90). The stamens of *Berberis* and *Mahonia* are only sensitive to contact on the inner side near their base, and as their contraction occurs only on the inner side, the anthers are thus brought into contact with the stigma. Examples of variation movements of carpellary leaves may be seen in the flowers of *Mimulus*, *Strobilanthes* (*Goldfussia*), *Martynia*, *Torenia*, and other plants. The two lobes of the styles of these flowers fold together when irritated. Similarly, in the flowers of *Stylidium*, a sudden upward movement of the bent style occurs when it is irritated by a touch.

VI. Reproduction

The life of every plant is of limited duration. Death ensues, sooner or later, and the decayed remains form a part of the surface soil. All existing plants are descended from ancestral forms. A spontaneous generation of new organisms from lifeless matter does not, as far as experience teaches, take place, and all existing vegetable life owes its existence to the capacity inherent in all organisms of reproducing their kind. Reproduction is accordingly a vital power which must be exercised by every existing plant species. In special cases, it is true, abnormal forms, sports or monstrosities, are produced unlike their parent plants; but although they grow vigorously and develop a strong vitality, they have lost the capability of giving rise to equally strong descendants, or are unable to compete successfully with wild plants in the struggle for existence, and consequently would soon die out were they not protected and multiplied by artificial means. A great number of our cultivated plants belong to this class of artificially maintained plant forms.

It is also evident from the very nature of reproduction that in the production of new organisms a process of rejuvenation is continually being carried on.

The formation of independently existing offspring necessitates also their separation from the parent plant. The formation of a new bud by a tree would never be distinguished as reproduction so long as the bud remained in connection with the tree as a part of its life. But if the bud became separated from the tree and continued its existence as an independent plant, that would constitute a form of reproduction, and, in fact, this actually takes place in many plants.

The conditions of the outer world make the still further demand upon reproduction, that from it a multiplication of the species should result. As the germs after separation from the mother plant do not always find the conditions necessary for their development and so, for the most part, perish, the extinction of the whole species would soon result if a plant produced but a single germ. That in reproduction care is taken for the multiplication of the individual in an almost spendthrift manner, is shown by a consideration of the innumerable spores produced by a single mushroom, or by the thousands of seeds contained in the fruit capsule of an orchid.

REJUVENATION, SEPARATION, and MULTIPLICATION of the individual are accordingly the essential requisites of reproduction.

These requirements are fulfilled by plants in the most varied manner. Each great division of the vegetable kingdom has adopted its own special method; and each family and genus, or even the different species, are characterised by some peculiar feature of their manner of reproduction. Systematic botany is so essentially based upon the different development of the reproductive organs and their functions, that it consists for the greater part of special descriptions of the processes of reproduction in the vegetable kingdom.

Numerous and varied as these processes are, they are in reality but modifications of two different and distinct modes of reproduction.

The simpler of these, or VEGETATIVE REPRODUCTION, consists in the formation of cells or cell bodies which, after their separation from the parent plant without undergoing any further change, either germinate at once, or develop into new organisms after a period of rest. This mode of reproduction, in which the growth and development of the parent plant are directly continued, is also distinguished as MONOGENETIC, VEGETATIVE, or ASEXUAL reproduction.

In SEXUAL REPRODUCTION, the second of the two modes of propagating vegetable life, two kinds of reproductive cells are first formed, but neither is directly capable of further development, and both perish in a very short time, unless opportunity is given for their fusion with each other. Not until one cell (the female) has fully taken up and become inseparably united with the other cell (the male), does it acquire the capacity of development and growth. This mode of reproduction is designated SEXUAL or DIGENETIC reproduction.

The physiological significance of sexual reproduction is not at once apparent. In many plants the vegetative mode of reproduction is sufficient to secure the necessary multiplication of the species, so that plants are able to continue without sexual reproduction. Many Fungi, for instance, are reproduced only vegetatively; the cultivated Banana, many *Dioscoreaceae*, and varieties of the Grape, Orange, Strawberry, no longer reproduce themselves sexually, but are propagated solely in a vegetative manner. The Garlic, which forms small bulbs in place of flowers, the White Lily, and *Ranunculus Ficaria*, which reproduces itself by root tubers, are hardly able to produce good seeds, which can, however, be obtained by operative interference, *e.g.* on separated inflorescences ([91]). They multiply exclusively by asexual methods without suffering any degeneration. Continued reproduction by vegetative means used to be regarded as necessarily injurious ([92]).

Since monogenetic reproduction is sufficient for the preservation of the species, sexual reproduction must answer some purpose not attained by the vegetative mode of multiplication, for otherwise it would be altogether superfluous that the same plant, in addition to the vegetative, should also possess the sexual form of reproduction, which is so much more complicated and less certain. Even the Mould Fungus (*Mucor Mucedo*), whose vegetative spores (conidia) are very widely distributed, occasionally develops sexual reproductive cells in specially formed sexual organs.

In many of the lower plants (Algæ and Fungi) it has been shown that the development of sexual cells is dependent upon definite external influences. KLEBS has demonstrated, in fact, that it is possible by regulation of the external conditions (nutrition, temperature, transpiration, composition of substratum and of the surrounding medium) to induce them to produce at will either non-sexual swarm-spores or sexual cells ([93]). In many plants unfavourable external conditions apparently give the impetus to a sexual mode of reproduction. The sexual product (zygospores of Algæ, Phycomycetes) seems better able than the vegetative germs (swarm-spores of Algæ, conidia) to remain a long time at rest, and so withstand the disastrous effects of an unfavourable environment. No inference can be drawn, however, from the function of the sexual germs in this instance concerning the necessity for the existence of a sexual, in addition to a vegetative, mode of reproduction; for in other cases it is the vegetative reproductive bodies, as, for example, the spores of Ferns, which are especially equipped for a period of enforced rest.

What makes digenetic reproduction essentially different from monogenetic is the UNION OF THE SUBSTANCES OF THE PARENTS AND THE CONSEQUENT TRANSMISSION AND BLENDING OF THE PATERNAL AND MATERNAL PROPERTIES, a point which is especially clearly shown in hybrids (p. 287).

It is in this influence exerted upon the quality that the chief difference between sexual and vegetative reproduction is shown. BY VEGETATIVE REPRODUCTION THE QUANTITATIVE MULTIPLICATION OF THE INDIVIDUAL IS SECURED, WHILE BY SEXUAL REPRODUCTION A QUALITATIVE INFLUENCE IS EXERTED. The vegetatively produced progeny consist of unmixed descendants; the sexually produced offspring, on the other hand, are the result of a blending of the parents.

In vegetative multiplication the complex of properties unfolded in the descendants does not as a rule differ from that possessed by the parent form. By vegetative multiplication all the varieties and races of cultivated plants, the characters of which do not come true by seed, are maintained. Variation may, however, occur among the vegetatively produced progeny. The occurrence of this may be compared to bud-variation, in which a single bud on a tree may give rise to a branch deviating in colour and form from the type; such a bud-variation may, years after, return suddenly to the characters of the typical form. In the same way variations arise among vegetatively produced plants, a remarkable example of which, according to BEYERINCK, is afforded by the Bacteria, the reproduction of which takes place exclusively by diversion into two ([94]).

The sexually produced offspring, on the other hand, endowed with the properties of the father, can never be identical with the mother-plant but possess the properties of both parents. When these are divergent they frequently play very different parts in the descendants, some characters appearing conspicuously, while others become less marked or remain completely latent. In this way the descendants do not exhibit a uniform mean between the parents, but some may resemble the father, others the mother. Variations appearing in single individuals will, unless they are of an absolutely dominating character, become modified and ultimately lost by crossing with ordinary individuals. In such a case sexual reproduction tends to maintain the constancy of the species. In other cases, as when both parents tend to vary in the same direction, the deviation from the ancestral form may be increased by sexual reproduction, as two systems of waves may reinforce one another if their periods coincide.

The great tendency to variation commonly exhibited by hybrids illustrates how the equilibrium of the complex of properties of a sexually produced individual is affected by divergent parental tendencies. But, even as a result of ordinary fertilisation, not only small and readily disappearing variations but sometimes more striking ones, in which the offspring differs so strongly from the parents in characters, which can be inherited, that it appears to be a new species or sub-species, occur. Of such *petites espèces* of *Draba verna* some two hundred are known. In such sudden variations (which v. KÖLLIKER, and with him KORSCHINSKY, term heterogenesis, while DE VRIES more recently calls them mutations) these authors seek the starting-points of the origin of new species. This would occur when a particular species passes, from unknown causes, into a period of mutation such as DE VRIES demonstrated experimentally in *Oenothera lamarckiana.* KORSCHINSKY collected a number of historical examples of heterogenesis, of which *Chelidonium laciniatum*, which appeared in a garden at Heidelberg in 1590, and *Capsella Heegeri*, SOLMS, which only recently appeared, will serve as examples (95).

The experience of cultivators and the recent experimental work on lower plants carried out by KLEBS show that different groupings of the internal and external conditions of life favour reproduction and ordinary growth respectively. In fact growth and reproduction appear to be mutually exclusive.

Vegetative Reproduction

Vegetative reproduction, the purely quantitative character of which as a mere process of multiplication has been emphasised, exists generally throughout the vegetable kingdom, and but few plants, *e.g.* some of the Conifers and Palms, are altogether devoid of it. Mention has already been made in considering artificial propagation that, from the separate parts or single cells, or even from the naked energides (*Siphoneae*) of many plants, the regeneration of a new and perfect individual may ensue. In vegetative reproduction the process is similar except that the separation of the part from the parent plant is an organic one, occurring in the natural course of development. The vegetative form of reproduction is manifested in various aspects, and may be distinguished as a multiplication by means of multicellular vegetative bodies (budding), or by single cells (spore-formation).

Multiplication by Multicellular Vegetative Bodies (Budding) often consists merely in the separation of lateral shoots, or in a division of a single plant into several. In this way the lateral shoots of the Water Fern, *Azolla*, through the death and disruption of the older parts of the parent axis, become separated from one another and continue their growth as independent plants; similarly, separate plants originate from the vegetative body of the Duckweed (*Lemna*).

Multiplication by stolons, rhizomes, and tubers results in a similar formation of independently existing plants. As may be seen in the Strawberry, Potato, *Ranunculus repens*, etc., the shoots produced from many of the axillary buds of the widely outstretched stolons take root and form new plants. In cases where the runners themselves eventually die, the parent plant becomes finally surrounded by a colony of entirely independent plants. Instead of forming runners, the single tuber may divide (*Corydalis solida*), and in this way give rise to two, four, or more new tubers. New bulbs are produced in the leaf-axils of the bud-scales of bulbs, while brood buds (bulbils, gemmæ) are frequently developed on aerial vegetative organs.

Bulbils are found on the inflorescence in the place of the flowers in many species of *Allium*, in the grass *Poa bulbifera*, and also in *Polygonum viviparum*. In *Lilium bulbiferum*, *Dentaria bulbifera*, etc., the bulbs in the axils of the leaves are specially constructed with a view to detachment from the parent plant (Fig. 22). The swollen leaves contain reserve food material, and frequently develop roots before falling from the plant. In *Ranunculus Ficaria* the roots of the axillary buds are full of reserve food material, and resemble grains of corn. When the plant dies the bulbils remain on the ground, and have given rise to the fable of showers of grain. Bulbils or gemmæ are met with also among the Mosses, Liverworts, and Ferns. The winter buds of many water plants (*Hydrocharis*, *Utricularia*, *Lemna*, etc.) have a peculiar biological significance. They are formed in the autumn, and sink to the bottom of the water; in the succeeding spring they rise to the surface and form new plants.

By vegetative multiplication higher plants can annually give rise to individuals which are strong and capable of flowering and fruiting. The seedlings of such plants, on the other hand, often require to grow for several years before the capacity of sexual reproduction is attained (bulbous plants, Hop, etc.).

In addition to the instances just cited, in which the vegetative reproductive bodies take their origin from points where lateral shoots are normally formed, they may also appear in places where no shoots are normally developed. Thus the adventitious formations often found on leaves, particularly on the leaf-blades, serve the purpose of reproduction. Just as the leaves of the *Begonia*, after they have been cut off, are able to give rise to new plants, in other cases the leaves possess this power while still growing on the parent plant. Some Ferns afford specially characteristic examples of this (*Asplenium decussatum*, *A. Fabianum*, *A. bulbiferum*, *A. viviparum*); adventitious buds are produced on their laminæ, developing into small rooted plants, which then fall off and complete their development (Fig. 216). The adventitious buds of *Cystopteris bulbifera* take the form of bulbils with small swollen leaves. Adventitious plantlets are frequently formed also on the leaves of *Cardamine pratensis*, and *Cardamine amara* manifests a similar tendency. One of the best-known examples of such adventitious formations is afforded by the leaves of the tropical *Bryophyllum*, in whose marginal indentations the brood plantlets develop in great numbers. Gemmæ are abundantly produced on the thallus of many *Hepaticae* (*Marchantia*, *Lunularia*), and by their continuous growth the gemma cups (Fig. 320, *b*) are always kept well filled.

FIG. 216.—*Asplenium Fabianum*. A young plant (*T*), with leaves and roots (*W*), has sprung from the leaf (*M*) of the older plant.

A most remarkable instance of adventitious budding sometimes occurs, in which adventitious buds, which have arisen in the nucellus of the ovule, grow into the embryo-sac, and there develop just as if they were embryos; examples of this phenomenon may be found in *Evonymus*, *Citrus*, *Funkia* (Fig. 217), *Coelebogyne*. Formerly it was thought that such a POLYEMBRYONY was due to the existence of numerous egg-cells in one embryo-sac; but STRASBURGER has shown, however, that it arises from the vegetative formation of ADVENTITIOUS GERMS. At the same time the egg-cell previously existing in the embryo-sac is able to continue its development after fertilisation, but is usually prevented from so doing by the adventitious or nucellar embryos. The seeds in such cases would no longer contain the products of sexual reproduction, but would be degraded to organs of vegetative multiplication. The adventitious germs in the polyembryonic seed are, however, so far dependent upon sexual reproduction, that for the most part they only attain their development in case pollination has previously taken place; but in *Coelebogyne*, one of the Australian *Euphorbiaceae*, of which usually only female specimens are found in cultivation, and in *Balanophora elongata* according to TREUB, and *Bal. globosa* according to LOTSY (96), the adventitious germs develop without the stimulus of fertilisation. This plant, accordingly, affords another example of APOGAMY, or of the substitution of a vegetative for a sexual mode of reproduction, such as occurs in different degrees in certain Ferns, *Athyrium filix femina* var. *cristatum*, *Aspidium falcatum*, *Todea africana*, and *Pteris cretica*. In the last-named example the sexual organs are no longer formed, although the young plants arise, by a vegetative process of budding, from exactly the same part of the prothallium where the archegonia would have been developed. In the case of *Aspidium filix mas* var. *cristatum* the apogamy seems to have resulted from cultivation. In a broad sense the development of bulbils in the place of flowers, in the species of *Allium*, might be considered as an example of apogamy.

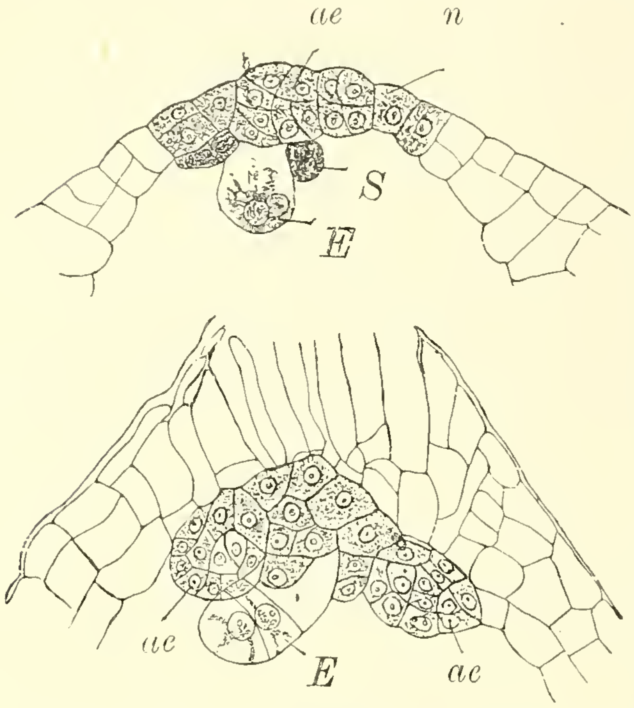


FIG. 217.—Vegetative formation of embryos in *Funkia ovata* (*Hosta coerulea*) by the budding of the nucellus; *n*, nucellus with cells in process of forming the rudiments (*ae*) of the adventitious embryos; *S*, synergidæ; *E*, egg-cell, in the lower figure developing into a sexually-produced embryo. (After STRASBURGER.)

Parthenogenesis, or the development of an egg-cell without previous fertilisation, might also be viewed as an instance of the same phenomenon in plants with more advanced sexual differentiation. In *Chara crinita* parthenogenesis has been positively proven. The female plants of this species of *Chara* are widely distributed throughout Northern Europe, and develop normal plants from their egg-cells, although the male plants are found only in Asia and in South Europe, so that fertilisation could not have taken place. Parthenogenesis is also known in some species of *Saprolegnia* and *Marsilia*. JUEL has proved its occurrence in *Antennaria dioica*, and MURBECK in the genus *Alchemilla* (Tribe *Eu.-Alchemilla*, *A. alpina*, *A. vulgaris*, *A. speciosa*, etc.). In these cases fertilisation is excluded by the complete degeneration of the pollen, and the first embryonic divisions take place before the flower-bud has opened. More extended observations will doubtless reveal other cases of parthenogenesis ([97]).

The observation made by LOEB, WINKLER, NATHANSOHN, and others, that the stimulus to formation of the embryo can be given in other ways than by copulation with the male cell is of special interest. LOEB found that solutions which withdrew water ($MgCl_2$, other salts, sugar, urea) could stimulate the ovum to parthenogenetic development. WINKLER used extractives derived from the sperm, while NATHANSOHN showed that sometimes a rise of temperature could interrupt the resting state of an ovum awaiting fertilisation and lead to a parthenogenetic development ([98]).

Vegetative Multiplication by Single Cells (Spore-Formation).—As in the case of multicellular vegetative bodies, multiplication can be effected also through the separation of single cells. Strictly speaking, this manner of multiplication actually takes place whenever a division of the vegetative body occurs in unicellular Bacteria, Fungi, and Algæ. Cells which serve the purpose of vegetative reproduction, and have a special form and method of development, are first met with in the higher Cryptogams. They are frequently formed in special organs or receptacles (sporangia, conidiophores, fruit bodies, cf. the special part).

As a Fern-plant occasionally arises directly from the tissue of the prothallus without the intervention of the sexual act, so also spore formation is occasionally omitted, and the prothallus arises vegetatively from the leaf of the sporophyte (apospory in varieties of *Athyrium*, *Aspidium*, etc.).

Sexual Reproduction

For the purpose of sexual reproduction two kinds of cells, male and female, are produced. Although neither alone is as a rule capable of development, the actual reproductive body is formed by the fusion into one cell of two such sexually differentiated cells.

In fertilisation two uninucleate cells fuse, even when the vegetative protoplasts are multinucleate. In *Albugo Bliti*, however, STEVENS found that the numerous nuclei of the ovum fused with an equal number of sperm nuclei. Probably other cases of this kind may be found ([99]).

In connection with parthenogenesis it was noted above (p. 278) that the incapability of further development which characterises the unfertilised ovum may be overcome by other means than copulation with the male cell; KLEBS had already shown this to be the case with the gametes of certain *Algæ* ([100]). It is thus necessary to distinguish in fertilisation between a stimulus, which removes the arrest laid on the further development of the ovum, and the cell fusion, which influences the nature of the resulting organism. The two influences are united in the case of natural fertilisation.

As it is thus necessary in sexual reproduction not only to provide for the production of male and female cells, but also to ensure their union, it becomes at once evident that, for sexual reproduction, the organs must have a different morphological and anatomical structure than if they were designed solely for vegetative activity. The sexual organs accordingly often exhibit a special and peculiar form, which differs materially in appearance from the vegetative parts of a plant.

The Union of Sexual Cells (Fertilisation).—Leaving out of consideration the necessary external contrivances to that end, fertilisation is accomplished by means of a chemotactic or chemotropic stimulus (pp. 242, 261). It is generally the non-motile egg-cells or female sexual organ which exert an attractive influence upon the motile male cells. When, however, there is no difference in the external form of the male and female cells, then both are usually motile, and the attraction seems to be exerted mutually. This is probably the case with the motile and externally similar sexual cells (GAMETES) of the lower Cryptogams, particularly of the Algæ (Fig. 96). In the conjugation of the *Conjugatae*, however, although both sexual cells are externally alike, one cell alone is usually motile, and passes through the connecting canal to the other. This capacity of the male cells for independent movement is common to most Algæ, with the exception of the *Florideae*, in which the walled male cells are passively conveyed to the female organ by the water. Throughout the whole group of the higher Cryptogams, and in a few Gymnosperms, the male cells are motile spermatozoids, capable of seeking out the non-motile egg-cells concealed within the archegonia. But in the sexually differentiated Fungi the male substance usually remains enclosed in special hyphæ which press themselves close against the female organs, and, by the perforation of the intervening cell wall, the fusion of their contents is rendered possible. The fertilisation of the Phanerogams is accompanied by a perforation of the intervening cell walls similar to that which occurs in the Fungi. In this case the male cell is enclosed within the pollen grain; the female, as a naked egg-cell, is included in the embryo-sac, which in turn lies in the ovule, and in the Angiosperms the ovule is again enclosed within the ovary. The double-walled pollen grains possess no independent power of movement, but are conveyed to the female sexual organs by the assistance of external agencies (animals, currents of air or water). The pollen grain then grows out into a tube which is acted upon by chemotropic (including hydrotropic and aerotropic) influences, and grows like a fungus-filament through the tissues of the ovary and ovule until it penetrates to the egg-cell in the embryo-sac; whereupon the union of the sexual cells is easily effected (Fig. 98).

Recent researches have shown that in addition to the fusion of the generative cell with the ovum the second generative cell frequently fuses with the nucleus of the embryo-sac. The endosperm, which arises from the resulting nucleus, is thus, like the embryo itself, a product of fusion. It is uncertain whether any biological significance is to be attached to this so-called double fertilisation; more probably the explanation is that the embryo-sac cell, as a sister cell of the ovum, exercises a similar chemotactic influence, and thus attracts the generative cell, the fusion being of secondary importance since the endosperm is destined to be used as food by the embryo ([101]).

While one healthy pollen grain should be able to fertilise one healthy ovule, experience shows that better results follow from more liberal pollination of the stigma. This depends, according to CORRENS ([102]), on the fact that not every pollen grain (and not every ovule) is good. Thus in *Mirabilis jalapa* for each fertile pollen grain four are found infertile, and for every three good ovules there is one bad one. For *Mirabilis longiflora* the corresponding ratios are 1 : 3 and 1 : 1.

To render certain the accomplishment of this POLLINATION, or conveyance of the pollen to the female sexual organs, special and often complicated contrivances are made use of by the different Phanerogams, according to the means of conveyance upon which they are dependent ([103]).

Plants, the pollen of which is carried by wind, are designated ANEMOPHILOUS. As this method of conveyance depends upon the chance of wind direction, the production of an enormous amount of pollen characterises wind-fertilised plants.

Such enormous quantities of pollen are often taken up from pine forests by the wind that clouds of pollen fill the air. The surface of Lake Constance in spring is so thickly covered with pollen that it is coloured yellow ("the lake blooms," it is then said), and in the Norwegian fiords, at a depth of 200 fathoms, the pollen of Conifers, according to F. C. NOLL, forms for a time the principal nourishment of the Rhizopod *Saccamina*.

The male flowers of such anemophilous plants are accordingly either freely exposed to the wind in Catkins (*Coniferae*, *Amentaceae*), or the versatile anthers, as in the Grasses, depend from long, lightly-swaying filaments. The pollen grains themselves do not stick together but escape from the opened anthers in the form of fine powder. The pollen grains of many Conifers are rendered extremely buoyant and easy of conveyance by the wind by two sac-like protrusions of the exine. In some anemophilous plants the pollen is discharged by the sudden extension of the filaments, previously rolled up in the bud (*Urticaceae*, *e.g. Pilea*), or by the hygroscopic tension of the anthers. The female organs are also often especially adapted for the attachment of the pollen thus floating in the air. The stigmas either spread out like a brush (*Corylus*), or are finely feathered or provided with hairs (Grasses, Walnut), or drawn out into long threads (Indian Corn). In the Conifers, with freely exposed ovules, the grains of pollen are caught and retained in a drop of fluid exuded from the micropyle, into which they are gradually drawn as the fluid dries up. In other Conifers whose ovules are concealed in the cone of the female inflorescence, scale-like formations catch the pollen and conduct it to the sticky opening of the young ovules.

For the fertilisation of the higher plants, the presence of water is not so essential as it is for most Cryptogams. Only a few submerged Phanerogams make use of the agency of water for effecting their pollination, and are, on that account, termed HYDROPHILOUS PLANTS (^{104}). The pollen of the submerged *Zostera* exhibits certain peculiarities, distinctly referable to the necessity of effecting fertilisation under water. It does not form round grains, but in their place elongated thread-like filaments devoid of an exine, which, as they have the same specific weight as the surrounding water, are easily set in motion by the slightest currents, and are thus brought into contact with the stigmas. In the case of the submerged water plants, *Vallisneria*, *Elodea*, and species of *Enhalus* found in the Indian Ocean, the pollination is accomplished on the surface of the water. Thus, for example, the male flowers of *Vallisneria*, after separating from the parent plant, rise to the surface of the water, where they open and float like little boats to the female flowers, which, by the elongation of their spirally coiled flower-stalks, ascend, at the same time, to the surface of the water, only to become again submerged after fertilisation.

In the great majority of Phanerogams pollination is effected by means of animals. By enticing in various ways insects, birds, or snails, plants are enabled not only to utilise the transporting power but also the intelligence of animals in the service of pollen-conveyance. The pollination is then no longer left to chance; and as the transport of pollen to the sexual organs becomes more assured, the necessity for its formation in such enormous quantities as in anemophilous plants is obviated. For the most part, such plants (Figs. 219, 220) are adapted to POLLINATION BY INSECTS (ENTOMOPHILY). For their nourishment, plants offer not only the sugary sap, which, as nectar, is excreted from different parts of the flowers, but also the pollen itself, which furnishes a nitrogenous food material, and which, together with the honey, is kneaded by bees into bee-bread. As additional means of enticement, and to attract animals from a distance to the nectar offered by the sexual organs, special perfumes and conspicuous colours have also been developed. The ATTRACTIVE-APPARATUS of plants is generally formed by the coloured floral leaves; by the outer floral leaves or calyx (*Nigella*, *Aconitum*), or by the perianth (Lily, Tulip), or by the hypsophyllary leaves and parts of the shoot, which do not belong strictly to the flower (*Astrantia major*, *Richardia aethiopica*, *Melampyrum*, *Dalechampia*, *Bougainvillea spectabilis*). The pollen of the entomophilous, in contrast to that of the anemophilous plants, is not a dry powder, but its grains are stuck together with an oily or mucilaginous fluid; in other cases, they are held together by their rough outer surfaces and can only be removed from the anthers by animals. The structure of the flower is so contrived, as CHRISTIAN CONRAD SPRENGEL first pointed out in 1793 in his famous work on the structure and fertilisation of flowers ("Das entdeckte Geheimniss der Natur im Bau und in der Befruchtung der Blumen"), that the pollen grains must necessarily become attached to certain parts of the body of the animal visiting it in search of food, and so be conveyed to the sticky or hairy stigma of other flowers. The variety of means employed to secure pollination, and the wonderful adaptation shown by the flowers to the form and habits of different insects, are most remarkable. In addition to the stimulus of hunger, plants utilise the reproductive instinct of animals for securing their pollination. Not a few plants (*Stapelia*, *Aristolochia*, and members of the *Araceae*), by the unnatural colour of their flowers, combined with a strong carrion-like stench, induce carrion-flies to visit them and deposit their eggs; in so doing they effect, at the same time, the pollination of the flowers. In South America, instead of insects, it is the humming-birds which are especially active in the conveyance of pollen, as they seek for insects in the flowers; a starling visits the flowers of species of *Puya* to drink the watery nectar. In the Old World the honey-birds play a similar part. Species of *Feijoa* have sweet succulent perianth leaves to attract the birds, which serve to convey the pollen (105). Besides these ORNITHOPHILOUS plants there are a few visited by Bats (CHIROPTEROPHILOUS); thus the diœcious pandanaceous plant *Freycinetia* is pollinated by a Flying Fox (*Pteropus*), which eats the inner bracts. Pollination in some cases is effected by means of snails (MALACOPHILOUS PLANTS). To their instrumentality the flowers of *Calla palustris*, *Chrysosplenium*, and also the half-buried flowers of the well-known *Aspidistra* owe their pollination.

Self and Cross Fertilisation.—It has already been pointed out that it is by sexual reproduction, in contrast to the vegetative mode of multiplication, that qualitative modifications are effected. Such qualitative changes are best attained when the sexual cells are derived from different individuals. It is in accordance with this same principle that, in the sexual reproduction of plants, varied and often complicated contrivances are manifested, which conduce to CROSS-FERTILISATION (union between sexual cells of different individuals), even when the individuals themselves are HERMAPHRODITE and possess two kinds of sexual organs, as in the case of the majority of Phanerogams.

As, however, self-fertilisation takes place also in a small number of plants, either regularly or as a make-shift, it is evident that whatever may be the advantage derived from a union of two distinct individuals, it is no more essential for sexual reproduction than for vegetative multiplication. In consideration of the otherwise predominant tendency to cross-fertilisation, however, self-fertilisation, just as apogamy, appears to be a retrogression. Self-pollination, although regularly occurring, frequently fails to occasion self-fertilisation, as often the pollen will not develop pollen-tubes on the stigmas of the flower (self-sterile) by which it was produced, but only on those of different flowers (*Secale cereale*, *Corydalis cava*, *Lobelia fulgens*, *Verbascum nigrum*, etc.) (106).

The antipathy between the sexual organs of the same flower, in certain plants, so greatly exceeds the bounds of indifference that they act upon each other as poisons. Thus, for example, it is known of certain Orchids that pollination with their own pollen causes the death of the flower, while in other cases the pollen is killed in a short time by the stigmatic fluid.

In other instances, self-fertilisation occurs where cross-pollination either is not effected, or else in conjunction with it (Wheat, Barley, *Canna*, *Viola* species, *Linum usitatissimum*, etc.). By many plants, in addition to the large flowers adapted to insect pollination, small, inconspicuous flowers are produced which, usually concealed underground or by the lower leaves, never open, and only bear seeds which have been produced by self-fertilisation. In such flowers the stamens no longer open, the pollen-tubes growing through the wall of the anther to reach the stigma. In some plants the majority of the seeds are derived from such CLEISTOGAMOUS flowers (*Viola*), and sometimes their seeds alone are fruitful (*Polycarpum tetraphyllum* possesses only cleistogamous flowers). As the greater number of such plants, however, in addition to the seeds of the self-fertilised small cleistogamous flowers, produce others resulting from the cross-fertilisation effected in the larger flowers (*Impatiens noli-tangere*, *Lamium amplexicaule*, *Specularia perfoliata*, etc.), the ancestral plants of the cleistogamous generations, as well as their descendants, have, at least, the opportunity for cross-fertilisation open to them.

Special contrivances for ensuring the crossing of the sexual cells, particularly by preventing self-pollination, are found to exist throughout the whole vegetable kingdom.

Self-pollination is most effectually avoided when the plants are unisexual, that is when both male and female plants lead a separate existence. Such DIŒCIOUS plants exist in almost all classes of plants from the lower Cryptogams to the most highly developed Phanerogams (many of the lower Algæ, species of *Fucus*, *Marchantia*, *Polytrichum*, *Equisetaceae*, *Taxus*, Hemp, Hops, Date-Palm, etc.). In MONŒCIOUS plants the male and female organs occur on different flowers, but the flowers are borne on the same plants. The fertilisation between different flowers is thus secured; but even here crossing with other individuals is, for the most part, assured by dichogamy.

The term DICHOGAMY is used to denote the fact that the male and female sexual organs attain their maturity at different times. When either the male or female sexual organ matures before the other, the self-pollination of morphologically hermaphrodite flowers is avoided and crossing ensured. Both hermaphrodism and monœcism are more advantageous than diœcism, as all the plants in such cases are able to produce seeds; while in diœcious plants the male flowers cannot be utilised for the direct production of seeds. Dichogamy secures crossing in such a simple manner, and is so easily attained by hermaphrodite plants, that it is of very general occurrence in the vegetable kingdom. According to the priority of the maturity of their sexual organs, plants are designated PROTANDROUS or PROTOGYMOUS.

PROTANDRY, the earlier maturing of the male sexual organs, is the more frequent form of dichogamy. It occurs in the flowers of the *Geraniaceae*, *Campanulaceae*, *Compositae*, *Lobeliaceae*, *Umbelliferae*, *Malvaceae*, and in *Epilobium*, *Digitalis*, etc. The anthers, in this case, open and discharge their pollen at a time when the stigmas of the same flowers are still imperfectly developed and not ready for pollination. Accordingly, PROTANDROUS FLOWERS CAN ONLY BE FERTILISED BY THE POLLEN OF YOUNGER FLOWERS.

In the less frequent PROTOGYNY the female sexual organs are susceptible to fertilisation before the pollen of the same flowers is ripe; so that the PROTOGYNOUS FLOWERS MUST BE FERTILISED BY THE POLLEN OF OLDER FLOWERS (*Anthoxanthum odoratum*, *Luzula pilosa*, *Scrophularia nodosa*, *Aristolochia clematitis*, *Helleborus*, *Magnolia*, *Plantago media*, Fig. 218).

FIG. 218.—Inflorescence of *Plantago media* with protogynous flowers. The upper, still closed flowers (♀) have protruding styles; the lower (♂) have lost their styles, and disclose their elongated stamens.

A still more complicated method of effecting cross-fertilisation, because involving also morphological and anatomical differences of structure, results from HETEROSTYLY, or the peculiarity of some species of plants of producing stigmas and anthers which vary in height in different individuals of the same species. A good example of heterostyled flowers is afforded by the Chinese Primrose (Fig. 219). This plant has two forms of flowers, long-styled (*L*) and short-styled (*K*), while the positions of the stigmas and anthers in the two kinds of flowers are exactly reversed. The pollen grains of the short-styled flowers, moreover, are larger, and the stigmatic papillæ shorter, than in those with the longer styles (*p*, *P*, and *n*, *N*). The purpose of such morphological and anatomical differences existing between flowers of the same species was first

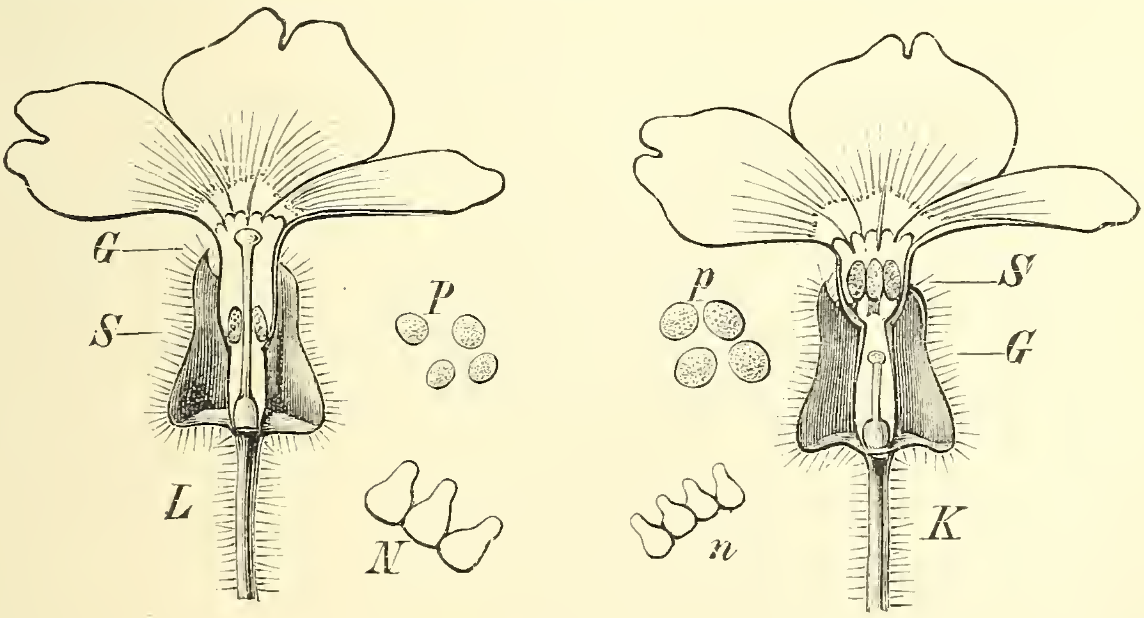


FIG. 219.—*Primula sinensis*; two heterostyled flowers from different plants. *L*, Long-styled; *K*, short-styled flowers; *G*, style; *S*, anthers; *P*, pollen-grains; and *N*, stigmatic papillæ of the long-styled form; *p* and *n*, pollen-grains and stigmatic papillæ of the short-styled form. (*P*, *N*, *p*, *n*, ×110.)

understood after they were discovered by DARWIN to be a contrivance for cross-pollination. Fertilisation is most successful in such cases when the pollination of the stigmas is effected by the pollen of anthers correspondingly situated. By such a "legitimate" fertilisation, more and better seeds are produced than by "illegitimate" fertilisation, and in some cases (*Linum perenne*, *Fagopyrum esculentum*) legitimate fertilisation alone is productive. Legitimate fertilisation is rendered more certain by the fact that insects in visiting the flowers touch correspondingly placed sexual organs with the same portions of their body. The flowers of Primroses have styles of two different lengths (DIMORPHIC HETEROSTYLY); the same peculiarity is exhibited by *Pulmonaria*, *Hottonia*, *Fagopyrum*, *Linum*. There are also flowers with TRIMORPHIC HETEROSTYLY (*Lythrum Salicaria*, and some species of *Oxalis*), in which there are two circles of stamens and three variations in the height of the stigmas and anthers.

In a great number of flowers self-pollination is made mechanically impossible, as their own pollen is prevented by the respective positions of the sexual organ from coming in contact with the stigma (HERCOGAMY). In the Iris, for example, the anthers are sheltered under the branched petaloid style, upon whose lip-like stigma no pollen can come, unless through the agency of insects, and in the flower of *Aristolochia clematitis* pollination from the anthers, which occupy a lower position on the column, is prevented. In the *Orchidaceae* and *Asclepiadaceae* self-pollination is rendered impossible both by the nature of the pollen masses and by their position. A complicated form of structural contrivance, by means of which cross-pollination is secured, may be seen in a flower of *Salvia pratensis* (Fig. 220). The anthers of this flower are concealed in the upper lip of the corolla, from which the style, with its bilobed stigma, projects. When a bumble-bee visits the flower in search of honey, it must first with its proboscis push out of the way the small plate (*s*), formed of two sterile anther halves grown together. These are situated at the ends of the short arms of the connectives (*c*), which are so elongated that they might easily be mistaken for the filaments (*f*) of the stamens. The fertile anther halves are situated at the other ends of the connectives, and so are brought in contact with the hairy back of the bumble-bee when it pushes against the plate at the short ends of the lever-like connectives. The pollen thus attached to the bee will be brushed off its back by the forked stigma of the next flower it enters. Good examples of

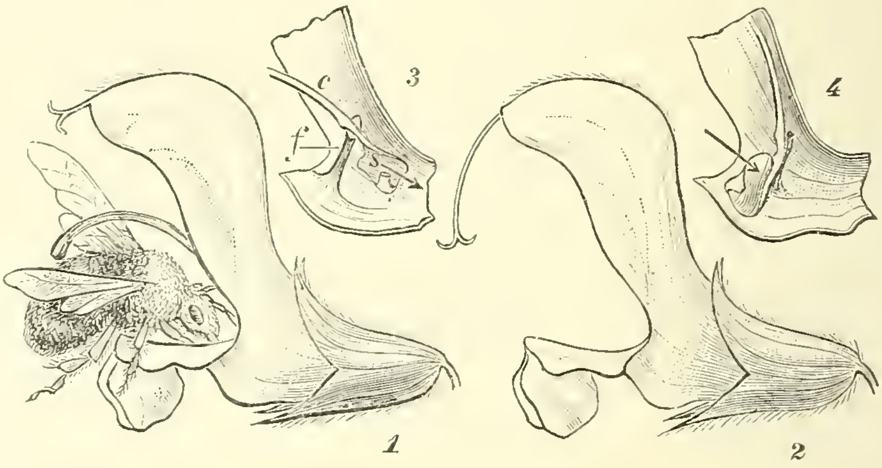


FIG. 220.—Pollination of *Salvia pratensis*. 1, flower visited by a bumble-bee, showing the projection of the curved connective from the helmet-shaped upper lip, and the deposition of the pollen on the back of the bumble-bee; 2, older flower, with connective drawn back, and elongated style; 4, the staminal apparatus at rest, with connective enclosed within the upper lip; 3, the same, when disturbed by the entrance of the proboscis of the bee in the direction of the arrow; *f*, filament; *c*, connective; *s*, the obstructing half of the anther.

hercogamous flowers are afforded by the *Papilonaceae*, by *Kalmia*, whose anthers are held in pockets of the corolla, by *Vinea*, etc.

Hybridisation.—The union of two sexual cells is, as a rule, only possible when they are derived from closely allied plants; it is only then that they exercise an attractive influence upon each other and fuse together in the act of sexual reproduction. The sexual cells of Mosses and Ferns, apart from all other considerations, would not unite because the spermatozoids of Mosses are attracted to the female organs by sugar, while those of the Ferns are only stimulated by malic acid. In the case of Phanerogams, a mixed union of sexual cells is likewise prevented by various obstacles to pollination and fertilisation. Occasionally, however, the sexual cells of different varieties, species, or even genera have shown themselves able to unite and produce descendants capable of development. Such a union is termed HYBRIDISATION, or bastard-formation, and its products HYBRIDS or BASTARDS.

Through the demonstration of the possibility of hybridisation, the sexuality of plants, for a long time doubted, was indisputably proven. (With this object in view, hybrids were raised in great numbers by KÖLREUTER as early as 1761) ([107]). It also demonstrated that the real purpose of sexual union was the combination of the properties of both parents, for transitional forms are found among hybrids which in many characteristics resemble the male and in others the female ancestor, or they may show an equal combination of the characters of both. Less frequently it happens that the hybrid resembles one ancestor almost exclusively. In such a case the attributes of the other ancestor remain latent, and may appear quite unexpectedly, through atavism (pp. 153, 275), in later generations. Had one species simple leaves and the other compound, their hybrid would have leaves more or less cleft; or were the flowers of one parent species red and those of the other yellow, the hybrid frequently bore flowers with red and yellow markings (mosaic hybrids), or which were orange-coloured. If an early blooming form were crossed with a late bloomer, the hybrid would flower at a time intermediate between the two. A large number of spontaneous hybrids have been found which have arisen naturally from plants with a special capacity for hybridisation. That such natural hybrids do not oftener occur is due to the lack of an opportune time or space for their development, and also to the fact that in the case of pollination of flowers with different kinds of pollen, that of their own species seems always more effectual in effecting fertilisation ([108]).

The more closely allied the parent plants, the more readily, as a rule, may hybrids between them be produced. Many families seem to incline naturally to hybridisation (*Solanaceae*, *Caryophyllaceae*, *Iridaceae*, etc.); others again develop hybrids only occasionally or not at all (*Cruciferae*, *Papilionaceae*, *Urticaceae*, *Convolvulaceae*, etc.). Even in the same family the related genera and species exhibit great differences in the readiness with which they may be crossed. The Grape-vine and also the Willow are easily crossed with other species of their own genus, and the same is also true of the different species of *Dianthus*, while the species of *Silene* cross with each other only with difficulty. Species hybrids are easily produced from species of *Nicotiana*, of *Verbascum*, and of *Geum*; on the other hand, it is very difficult to cross different species of *Solanum*, *Linaria*, or *Potentilla*. The hybridisation, however, of nearly allied forms is often impossible—the Apple with the Pear, for instance, although the Peach and Almond may be crossed, and also the species of even the different genera *Lychnis* and *Silene*, *Rhododendron* and *Azalea*, *Aegilops* and *Triticum*, each according to their "sexual affinity."

DERIVATIVE HYBRIDS arise when hybrids are crossed with one another, or with one of the original parent forms. In this way it has been possible to unite six species of Willow in one hybrid, and in the case of the Grape-vine even more species have been combined. It is only in rare cases, however, that the form of the hybrid remains constant in the succeeding generations. These exhibit more frequently a tendency to revert to one of the original ancestral forms.

In addition to their inherited qualities HYBRIDS EXHIBIT NEW PECULIARITIES not derived from their parent forms. These are a MODIFIED FERTILITY, GREAT TENDENCY TO VARIATION, and often a MORE LUXURIANT GROWTH. The fertility is often so enfeebled that the hybrids are sterile and do not reproduce themselves sexually. This enfeeblement of the sexuality increases the more remote is the relationship of the ancestral forms. The tendency to variability is often greatly enhanced in hybrids, especially in those arising from the hybridisation of different varieties of the same species. Hybrids, particularly those from nearly related parents, produce more vigorous vegetative organs, they bloom earlier, longer, and more profusely than the uncrossed plants, while at the same time the flowers are larger, more brilliant, and exhibit a tendency to become double. The luxuriance of growth and the increased tendency to produce varieties displayed by the hybrids have made the whole subject of hybridisation one of great practical as well as theoretical importance.

It is doubtful if hybrid forms can be produced (graft-hybrids) by a vegetative union of portions of two different plants (grafting, budding); in all properly regulated experiments the vegetatively united forms have preserved their independent individuality (p. 228).

The Dissemination and Germination of Seeds

If the seeds after their separation from the parent plant simply fell upon the earth, the young seedlings would be injuriously restricted to the place already occupied by the parent plant, and would also spring up in such large numbers that they would mutually exterminate each other. The dissemination of the seeds thus becomes a necessity, and although a larger or smaller proportion perish in the process, a small number eventually find themselves in a favourable environment.

For their DISSEMINATION, seeds make use of the same agencies as are employed for the conveyance of pollen. Thus their dispersion is effected by means of currents of air and water; by their forcible discharge from their receptacles; by animals; and also by their accidental transportation by railroads and ships.

To ensure the dispersal of seeds by the wind, all those contrivances are of use which serve to increase their superficial area with but small augmentation of their weight. Of this nature are the hairy appendages of seeds and fruit-walls, as in *Gossypium*, *Epilobium*, *Populus*, *Salix*, *Typha*, *Clematis*, and the fruits of the *Compositae* with their pappus, of *Valeriana*, etc. Compared with the accelerated fall in a vacuum, the retardation exerted by the resistance of the air (by which the opportunity for dispersal through the agency of the wind is enhanced) in the case of *Cynaria Scolymus* is, in the first second, as six to one. Similar adaptations for utilising the agency of the wind as a means of dispersal are the wing-like appendages formed from the expansion of the sepals (*Dipterocarpus*) or of the ovary (*Acer*, *Fraxinus*, *Ulmus*, *Polygonum*, *Robinia*, *Gleditschia*, and the fruits of many *Umbelliferae*), or of the seeds themselves, as in the winged seeds of the *Bignoniaceae* (and many *Ternstroemiaceae*). In a *Bignonia* seed (Fig. 221), with its widely outspread, glossy wings, the centre of gravity is so disposed that the seed floats lightly along through the air in an almost horizontal course, and with a motion like that of a butterfly. The seeds of *Zanonia*, one of the *Cucurbitaceae*, are very similarly equipped. In the Lime the subtending leaf which is attached to the inflorescence is retained to facilitate the dispersal of the fruits by the wind; and in the seeds of the Fir the winged appendages are derived from the tissue of the placental scale. The aerial transportation of seeds and fruits, winged only on one side, is accompanied by a continuous spirally twisting movement which assists to retard their fall. Thus in the above-mentioned *Bignonia* DINGLER found the retardation amounted to thirty times the free fall, and in *Pinus silvestris* to seven times (¹⁰⁹).

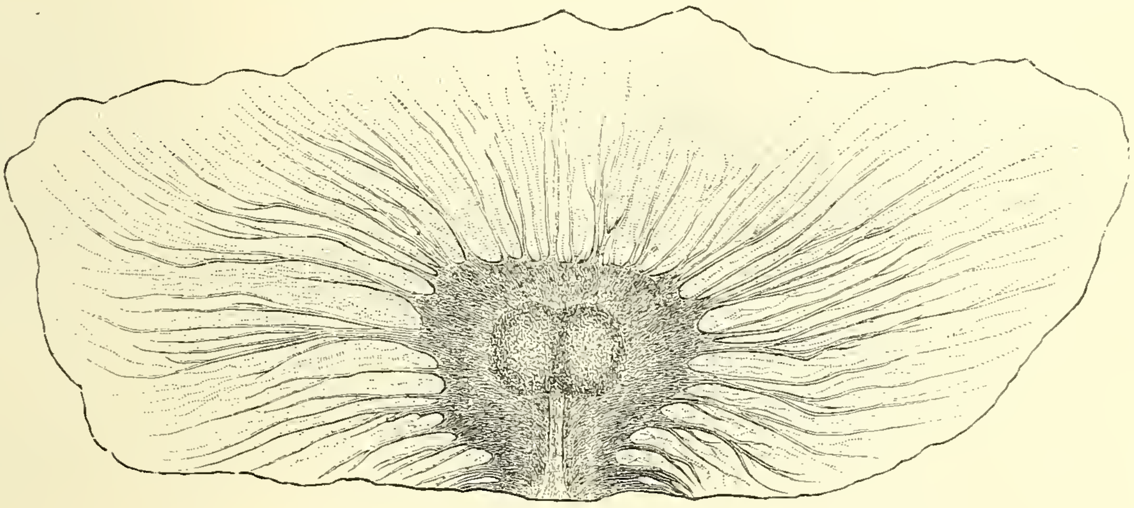


FIG. 221.—Winged seed of *Bignonia mucronata*. (Nat. size.)

The diminutive size of many reproductive bodies, and the proportionate enlargement of their surface in comparison with their volume, increase their buoyancy. Microscopically small Fungi, spores, and Bacteria are in consequence easily transported by the wind. In the spores of *Lycoperdon caelatum* DINGLER found the retardation to be as 1 to 1000, which, according to NÄGELI, could only be theoretically explained by the supposition that the retardation was intensified by a thin layer of air permanently adhering to the surface of the spores.

Seeds and fruit are also frequently transported great distances by the agency of WATER. In the case of maritime plants the seeds are often especially adapted (water-tight tissues; large air-spaces serving as swimming-bladders, etc.) for transport by ocean currents. Through the possession of such devices, the seeds of West Indian plants are carried to Norway by the Gulf Stream, and the appearance of Coco-nut palms as the first vegetation on isolated coral islands is in like manner due to the adaptation of their fruits to transport by water ([110]).

ANIMALS participate largely in the dissemination of seeds; either by eating the agreeably tasting and often attractively coloured fruit, and excreting the undigested seeds, or by their involuntary transportation of seeds and fruits which have become in some way attached to them. This is effected in many cases by hooks and bristles (*Lappa*, *Galium aparine*, *Bidens*, *Echinospermum*, *Xanthium*, and the fruits of *Medicago minima*, so common in sheep's wool and erroneously termed wool-lice). Or the seeds become attached to animals by means of some sticky substance; in this way the seeds of the Mistletoe, which stick to the beaks of birds eating the berries, finally adhere to the branches of trees upon which the birds wipe their bills. The widespread distribution of fresh-water plants can only be accounted for through the agency of aquatic birds.

The natural distribution of plants has been greatly modified by the interference of man, especially in these days of universal commercial intercourse by rail and sea. By their instrumentality not only have the useful plants been widely distributed over the earth, but the weeds have followed in the same way; and many a seed thus accidentally carried to other lands has finally found there a new place of growth.

The forcible discharge of spores and seeds is effected by the sudden liberation of hygroscopic or tissue tensions. It has already been mentioned that the capillitia of the Myxomycetes and the elaters of the Liverworts serve for the dispersal of the spores. In the case of the Box (*Buxus*), the smooth seeds are forcibly discharged by the contraction of the pericarp, like a bean pressed between the fingers. The dry fruit of *Hura crepitans* bursts apart with a report like that of a pistol, and is scattered in pieces far and wide. The turgescence and elasticity of the cell-walls give rise to the tension which results in the forcible discharge of the sporangia of *Pilobolus*, and in the ejection of the ascospores of many Ascomycetes. The bursting and rolling up of the segments of the seed-vessels of *Impatiens*, by means of which the dispersal of the seeds is effected, are due to the sudden release of tissue-tensions. Similarly, the fruits of *Momordica elaterium* and *Ecballium* dehisce suddenly and eject the seeds with considerable force. It is unnecessary to cite further examples; those already given may be sufficient to call attention to a few of the different means made use of for the dispersal of the reproductive germs.

Germination.—The dry condition of the seed and the cessation of all vital activity render the resting germ extremely resistant to the action of external influences, and capable of maintaining its vitality during the course of its dissemination, until it is ultimately fixed in the earth. In effecting their PERMANENT LODGMENT IN THE SOIL, seeds are aided by the various STRUCTURAL PECULIARITIES OF THEIR SURFACE (furrows, bristles, hairs, etc.). The fruits of the *Geraniaceae* (*Erodium*, Fig. 201) and *Gramineae* (*Stipa*, *Avena sterilis*, and species of *Aristida*) are enabled, by means of movements due to hygroscopic torsion, to bury themselves in the ground. In the case of *Trifolium subterraneum* and *Arachis hypogaea* the same result is accomplished by the geotropic growth of the fruit-stalks, while the seed-capsules of *Linaria cymbalaria* are deposited in the crevices of walls and cliffs by the negative heliotropic movements of the fruit-stalks. Nuts, acorns, and seeds buried by squirrels or other animals in the ground and forgotten, or for any reason not made use of, often germinate. The seedlings of Mangrove trees, *Rhizophora* and *Bruguiera*, exhibit a most peculiar manner of growth to ensure their lodgment in the ground. The seed germinates in the fruit before it is detached from the tree. When the radicle has attained a considerable length, the young seedling, separating either from the cotyledons or from the fruit-stalk, falls to the earth; it then bores into the mud, and is thus enabled to commence its growth without delay. Many seeds and fruits acquire a more or less voluminous MUCILAGINOUS SHEATH, which serves a double purpose. Quince seeds, Flax seeds, seeds of the Plantain, of Crucifers, the fruits of *Salvia Horminum*, seed of *Cuphea* and *Cobaea* (in the mucilage cells of which delicate thickening bands are rolled up), afford the best-known examples of such slimy envelopes, which, in addition to fixing the seed to the ground, serve to absorb water by holding it in their substance or drawing it in hygroscopically (cf. Mistletoe berries). Fruit-walls, by their spongy nature, may also serve as water-carriers (ripe fruits of *Tropaeolum*, *Poterium spinosum*, *Medicago terebellum*).

The germination of seeds, once securely lodged in the soil, may begin immediately or after a longer or shorter PERIOD OF REST.

The seeds of many Conifers do not germinate for several years. Some plants again, in addition to seeds which germinate in the first year, produce others which require a longer rest (*Trifolium pratense*, *Robinia Pseudacacia*, *Cytisus Laburnum*, *Reseda lutea*, etc.). Even under favourable circumstances such seeds do not germinate until a definite length of time has elapsed. Germination may be delayed also by external conditions, and the vitality of the seed may still be retained for years. Thus, for example, on the removal of a forest from land that had been under cultivation for forty-six years, PETER found that a great variety of field-plants at once sprang up as soon as the requirements for their germination were restored (111).

Germination, according to the observations of KLEBS, is introduced by true processes of growth, which result in THE RUPTURE OF THE SEED-COVERINGS (112). This is effected either by the growing radicle, or, in many Monocotyledons, by the cotyledon. In other seeds enclosed within a shell, the bursting of the shell through the growth of the endosperm or cotyledons precedes germination. In cases where the shell is very hard and does not consist of two halves easily separable by internal pressure (as in Cherry-stones), special places are often provided for the egress of the young seedling. At the end of a coco-nut, for example, such points of egress, behind the thinnest of which the embryo will be found emerging from the endosperm, are very easily seen. Through the extremely hard, thick shell of another Coco-palm, *Cocos lapidea*, there are three long germinal pores, while the seedling of *Acrocomia sclerocarpa* has only to push a loosely fastened plug out of the thick shell of the seed (Fig. 222) (113). Similar contrivances are found in the case of *Pandanus*, *Canna*, *Typha*, *Potamogeton*, and many Dicotyledons (*Tetragonia expansa*, *Medicago*, and some species of *Onobrychis* and *Portulaca*). SEEDLINGS PENETRATE THE SOIL by means of the elongation of the primary root, or of the hypocotyl, or also, as is the case with many Monocotyledons, through the movements of the geotropic cotyledons. After the descending part is firmly attached to the soil, by either root-hairs or lateral roots, THE UPWARD GROWTH COMMENCES. In this process the cotyledons may either remain within the seed (hypogeal) or unfold above ground (epigeal). The first is often the case where the cotyledons are full of reserve material (*Phaseolus multiflorus*, *Aesculus*, *Quercus*), or where their function is to absorb nourishment from the endosperm (in Palms and the scutellum of *Gramineae*). More frequently the cotyledons are pushed above ground, and may then be thick and filled with reserve nourishment, or thin and turning green on exposure to the light. In many Monocotyledons, as also in *Ricinus*, etc., the cotyledons, even if they afterwards appear above ground, may first take up the nutritive substances of the endosperm; while in the Conifers the cotyledons perform the same office above ground. THE COTYLEDONS ARE DRAWN FROM THE SEED by the curvature of the hypocotyl or of the petioles of the cotyledons (*Smyrnium*, *Delphinium*). The seed-coverings also are often further

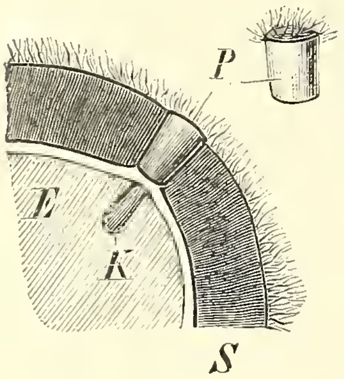


FIG. 222.—Section through the upper part of the fruit of *Acrocomia sclerocarpa*. *S*, The hard shell; *P*, the plug which is pushed out of the shell by the germinating embryo, *K*; *E*, endosperm. (After PFITZER.)

ruptured by the swelling of the hypocotyl (*Cucurbita*, etc.). The unfolding of the first leaves above ground is frequently accompanied by a CONTRACTION OF THE ROOT (114). This is caused by the cortical cells of the root becoming more stretched in a transverse than a longitudinal direction by their turgescence. The seedling is in consequence drawn deeper into the soil, and its position rendered more secure. Even older plants, particularly those whose leaves form a radical rosette, notwithstanding their upward growth, are held close to the ground through a similar contraction of their roots. According to the researches of RIMBACH the shortening amounts to 30 per cent of the length of root in *Allium ursinum*, to 50 per cent in *Arum maculatum*, and even to 70 per cent in *Oxalis elegans*.

When its attachment in the soil is properly provided for, and after the first germ-leaves are unfolded, the young plant has acquired the capacity for self-sustenance, its further growth and development being dependent upon its own activity.

PART II

SPECIAL BOTANY

SECTION I

CRYPTOGAMS

SPECIAL BOTANY

Special Botany is concerned with the special morphology and physiology of plants. While it is the province of General Botany to investigate the structure and vital processes of the whole vegetable kingdom, it is the task of Special Botany to interpret the structure and vital processes of its separate divisions. The aim of General Morphology is to determine the phylogenetic derivation of the external and internal segmentation of plants, and to refer their numerous structural peculiarities to the primitive form from which they have arisen. The purpose of Special Morphology, on the other hand, is to trace the development which has been reached in the different divisions of the plant kingdom, to understand the form of individual plants, and to trace the connection between one form and another. Thus the methods of special morphology are also phylogenetic, and furnish the basis for a natural system of classification of the vegetable organisms based upon their actual relationships. Although such a system must necessarily be very imperfect, as it is not possible to determine, directly and indisputably, the phylogenetic connection of different plants, but only to derive indirectly their relationships from morphological comparisons, the aim which we set before us is none the less both legitimate and essentially justifiable.

Such a natural system, founded on the actual relationship existing between different plants, stands in direct opposition to the artificial system, to which has never been attributed more than a practical value in grouping the plants in such a manner that they could easily be determined and classified. Of all the earlier artificial systems, the sexual system proposed by Carl Linnæus in the year 1735 is the only one which need be considered.

Linnæus, in establishing his classification, utilised characteristics which referred exclusively to the sexual organs, and on this basis distinguished twenty-four classes of plants. In the last or twenty-fourth class he included all such plants as were devoid of any visible sexual organs, and termed them collectively Cryptogams. Of the Cryptogams there were at that time but comparatively few forms known, and the complicated methods of reproduction of this now large class were absolutely unknown. In contrast to the Cryptogams, the other twenty-three classes were distinguished as PHANEROGAMS or plants whose flowers with their sexual organs could be easily seen. LINNÆUS divided the Phanerogams, according to the sexual character of their flowers, into such as possessed hermaphrodite flowers (Classes I.-XX.), and those in which the flowers were unisexual (XXI.-XXIII.). Plants with hermaphrodite flowers he again divided into three groups: those with free stamens (I.-XV.), which he further distinguished according to the number, mode of insertion, and relative length of the stamens; those with stamens united with each other (XVI.-XIX.); and those in which the stamens were united with the pistil (XX.). Each of the twenty-four classes was similarly subdivided into orders. While some of the classes and orders thus constituted represent naturally related groups, although by the method of their arrangement in the artificial system they are isolated and widely removed from their proper position, they include, for the most part, plants which phylogenetically are very far apart.

LINNÆUS himself (1738) felt the necessity of establishing natural families in which the plants should be arranged according to their "relationships." So long, however, as the belief in the immutability of species prevailed, the adoption of a system of classification expressive of relationship and family could have no more than a hypothetical meaning, and merely indicated a supposed agreement between plants having similar external forms. A true basis for a natural system of classification of organisms was first afforded by the theory of evolution.

The system adopted as the basis of the following description and systematic arrangement of plants is the natural system of ALEXANDER BRAUN, as modified and further perfected by EICHLER and others.

According to this system we have to distinguish between CRYPTOGAMS as the lower division, and PHANEROGAMS as the higher division of the plant kingdom.

SECTION I

CRYPTOGAMS

The Cryptogams include an extraordinary variety of the most different plant forms, extending from unicellular organisms to plants exhibiting segmentation into stem, leaf, and root. The Cryptogams, however, are collectively distinguished from Phanerogams by the mode of their dissemination by SPORES, in contrast to that of the Phanerogams, which is effected by SEEDS; spores are formed also by Phanerogams, but they are not the immediate cause of the origin and development of new individuals. Seeds are multicellular bodies, within which is included the multicellular rudiment or EMBRYO of a plant; while spores which, in the case of the Cryptogams, become separated from the mother plant, and give rise to a new and independent organism, are unicellular structures. Cryptogams may therefore be termed SPORE PLANTS or Sporophytes, and Phanerogams SEED PLANTS or Spermaphytes; although uniformity to previous usage and custom would recommend adherence to the older terms.

The Cryptogams are divided into the three following groups:—

I. The THALLOPHYTA, embracing a great variety of plants whose vegetative portion may consist of one or many cells in the form of a more or less branched thallus.

II. The BRYOPHYTA, which include forms with a leaf-like thallus, as well as cormophytic forms, with evident segmentation into stems and leaves. The Bryophytes possess no true roots, and their conducting bundles are of the simplest structure.

III. The PTERIDOPHYTA, or Fern-plants, exhibit a segmentation into stems, leaves, and roots, and also possess true vascular bundles. While thus resembling the Phanerogams in structure, they differ from them in their mode of reproduction, and in their dissemination by means of spores.

The Thallophytes and Bryophytes are also characterised as cellular plants, in contrast to the Pteridophytes or Vascular Cryptogams, which, together with the Phanerogams, are collectively designated Vascular Plants. Bryophyta and Pteridophyta must be regarded as having originated from the higher Thallophytes, the development of the two groups having been on different lines.

I. THALLOPHYTA

The Thallophytes may be divided according to their natural relationships into the following classes:—

1. *Flagellata*, Flagellates.
2. *Myxomycetes*, Slime-fungi.
3. *Bacteria*, Bacteria.
4. *Cyanophyceae*, Blue-green Algæ.
5. *Diatomeae*, Diatoms.
6. *Peridineae*, Dinoflagellates.
7. *Conjugatae*, Conjugates.
8. *Chlorophyceae*, Green Algæ.
9. *Phaeophyceae*, Brown Algæ.
10. *Rhodophyceae*, Red Algæ.
11. *Characeae*, Stoneworts.
12. *Hyphomycetes*, Fungi.

Excluding the Flagellates, which combine animal and vegetable characters, it was formerly customary to divide the Thallophyta into the two groups of Algæ and Fungi. The Algæ are Thallophytes which possess chromatophores with colouring pigments, particularly chlorophyll; they are, therefore, capable of assimilating and providing independently for their own nutrition. The Fungi, on the other hand, are colourless and have a saprophytic or parasitic mode of life. Such a method of classification, however, although possessing a physiological value, has no phylogenetic significance, as it does not express the natural relationships between the various groups. The classes 4-11 in the above scheme belong to the *Algæ*, while the *Myxomycetes*, *Bacteria*, and *Hyphomycetes* are classed as *Fungi*.

To the twelve classes of the Thallophytes may be added, as Class 13, the Lichens (*Lichenes*), in which the thallus affords an instance of a symbiosis of Algæ and Fungi. From a strictly systematic standpoint, the Fungi and Algæ composing the Lichens should be classified separately, each in their own class; but the Lichens, among themselves, exhibit such a similarity in structure and mode of life, that a better conception of their characteristic peculiarities is obtained by their treatment as a distinct class.

The classes distinguished above are on the whole sharply limited from one another, and little can be said with certainty of their mutual relations. The *Bacteria* and *Cyanophyceae* are isolated groups. The *Conjugatae* may be regarded as a branch from the common root of the *Chlorophyceae*, while the highly organised *Characeae*, and possibly the *Rhodophyceae* also, may have originated from more highly differentiated Green Algæ. The *Hyphomycetes* may be derived as colourless forms from *Chlorophyceae*, and perhaps also from *Rhodophyceae*. The Flagellate may be looked upon as representing the forms from which the primitive Green an Brown Algæ, as well as the Diatoms, *Peridineae* and *Myxomycetes*, were derived.

As a rule the Thallophytes are distributed and multiplied by means of asexually produced spores, but with a varying mode of development in the different groups; and also, although not in all classes, they exhibit a sexual mode of reproduction. This reproduction consists, in the simplest cases, in the production of a single cell, the ZYGOSPORE or ZYGOTE, by the union or CONJUGATION OF TWO SIMILARLY FORMED SEXUAL CELLS OR GAMETES. In many of the more highly developed forms, however, the gametes are differentiated as small male cells or SPERMATOZOIDS, and as larger female cells, the egg-cells or OOSPHERES. As a result of the fusion of an egg-cell and a spermatozoid, an OOSPORE is produced. The first form of sexual reproduction or fertilisation is termed ISOGAMOUS, the second OÖGAMOUS; but these are connected by intermediate forms. It must be assumed that the sexual cells have been derived in the phylogeny of plants from asexual spores, and that asexual multiplication has taken origin from simple cell division.

While the reproduction of some Thallophyta is exclusively asexual and of others exclusively sexual, in many others both forms of reproduction occur. In the latter case this may occur on the one plant, or separate successive generations may be distinguishable. Generally speaking, there is, however, no regular succession of asexual and sexual generations in Thallophytes, the mode of reproduction being to a great extent under the influence of external conditions (1). Only in the Red Seaweeds and some Fungi is there an alternation of a sexual generation (gametophyte) with an asexual (sporophyte), such as is found in all Bryophytes and Pteridophytes.

CLASS I

Flagellata (Flagellates) (²)

The Flagellata are a group of unicellular, aquatic organisms; they combine animal and vegetable characteristics, and may be regarded as the starting-point on the one side of unicellular Thallophytes, on the other of the *Protozoa*.

The protoplast exhibits contractile or amœboid movements, and is limited by a denser protoplasmic layer and not by a definite cell-wall. One or more cilia (flagella) are present as motile organs. The protoplast contains a nucleus, a pulsating vacuole, and in many species well-formed green, yellow, or brownish-yellow chromatophores. Such forms are able to assimilate, but at times they live as saprophytes or animals, as do the colourless forms throughout their lives. The power of absorbing solid particles may be present over the whole surface or be localised at one or two points which serve as mouths.

It has been shown that some species appear as colourless forms with reduced chromatophores or as chlorophyll-bearing forms, according to the changes in the conditions of nutrition (*e.g. Euglena gracilis*) (³).

Sexual reproduction is wanting. Multiplication takes place by longitudinal division, and in many species thick walled resting spores are produced.

CLASS II

Myxomycetes (Slime-Fungi) (⁴)

The Myxomycetes form an independent group of lower Thallophytes; in certain respects they occupy an intermediate position between plants and animals, and have in consequence also been termed *Mycetozoa* or Fungus-animals. They are represented by numerous species, and are widely distributed over the whole earth. In their vegetative condition the Slime-Fungi consist of naked masses of protoplasm, the PLASMODIA, containing numerous small nuclei but utterly devoid of chlorophyll. Glycogen occurs as a reserve substance, while starch is not found. The plasmodia (p. 53) are found most frequently in forests, upon soil rich in humus, upon fallen leaves, and in decaying wood. They creep about on the substrata, changing their form at the same time, and thrust out processes or pseudopodia, which may in turn coalesce. Their movements are regulated by the intensity of the light and heat to which they are exposed, and by the amount of moisture and nourishment supplied by the substratum. Although in the vegetative condition the plasmodia are negatively heliotropic and positively hydrotropic, these characteristics become changed when the process of spore-formation begins. The plasmodium then creeps out from the substratum towards the light and air, and, after coming to rest, is converted into single or numerous and closely contiguous fructifications, according to the genus. On the periphery of each fructification an outer envelope or PERIDIUM is formed; while internally the contents of the fructification separate into spores, each of which is provided with a nucleus, and enclosed by an outer wall. The isolation of the spores may take place on the conclusion of cell divisions (*Trichia*); in other cases (*e.g. Fuligo*) the plasmodium divides into a number of multinucleate portions while nuclear division is in progress, and these portions subsequently divide, giving rise to the spores. The spores thus formed have accordingly an asexual origin. In many genera, part of the internal protoplasm within the SPORANGIUM or spore-receptacle is utilised in the formation of a CAPILLITIUM (Fig. 224, *B*), consisting of isolated or reticulately united threads or tubes. Upon the maturity of the spores, the peridium of the sporangium becomes ruptured, the capillitium expands (Fig. 223, *B*), and the spores are dispersed by the wind. In the case of the genus *Ceratiomyxa*, the process is somewhat simplified, as the fructification is not enveloped by a peridium, and the spores are produced at the extremities of short stalks. SEXUAL REPRODUCTION is entirely absent in the Myxomycetes.

A good example of the development of the plasmodia from the spores is afforded by *Chondrioderma difforme*, a Slime-Fungus common on decaying leaves, dung, etc., upon which it forms small, round, sessile sporangia. The germination of the spores (*a*, Fig. 59) may be easily observed when cultivated in an infusion of Cabbage leaves or other vegetable matter. The spore-wall is ruptured and left empty by the escaping protoplast. After developing a flagellum or CILIUM as an organ of motion, the protoplast swims about in the water, being converted into a SWARM-SPORE (Fig. 59, *c-g*), with a cell nucleus in its anterior or ciliated end, and a contractile vacuole in the posterior end of its body. Eventually the cilium is drawn in, and the swarm-spore becomes transformed into a MYXAMŒBA, which has the capacity of multiplication by division. In conditions unfavourable for their development they surround themselves with a wall, and as MICROCYSTS pass into a state of rest from which, under favourable conditions, they again emerge as swarm-spores. Ultimately a number of the Myxamœbæ approach close together (Fig. 59, *l*) and coalesce, forming small plasmodia (Fig. 59, *m*), which in turn fuse with others into larger plasmodia (Fig. 59, *n*); no nuclear fusion accompanies this coalescence. Both the amœbæ and plasmodia are nourished by the small food particles taken up by the protoplasm, which also exhibits active, internal, streaming movements. After an interval of a few days the plasmodium creeps to the surface of the substratum to the air and light, and passing into a resting stage

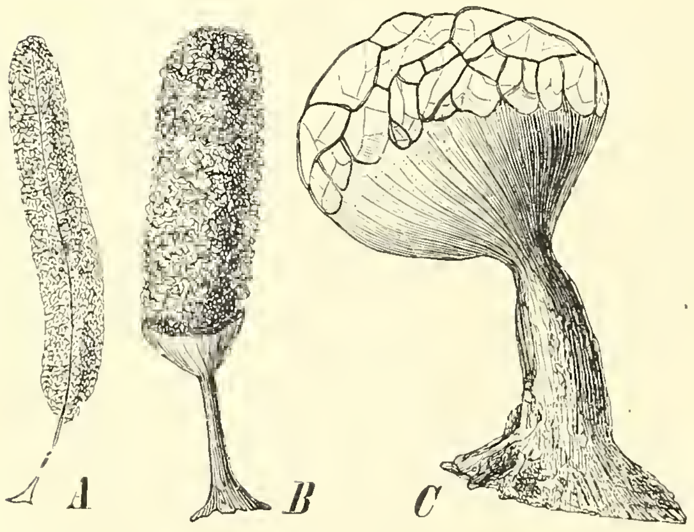


FIG. 223.—Ripe fructifications, after discharge of the spores. *A*, *Stemonitis fusca* (× 10); *B*, *Arcyria punicea* (× 12); *C*, *Cribraria rufa* (× 32).

becomes at length converted into a white sporangium with a double wall, consisting of an outer, calcareous, brittle peridium and an inner and thinner enveloping pellicle which, in addition to the numerous spores, encloses also a poorly developed capillitium.

The development of the other Myxomycetes is accomplished in a similar manner. Very large plasmodia, often over a foot in breadth, of a bright yellow colour and creamy consistency, are formed by the tan-pit Fungus *Fuligo varians* (*Aethalium septicum*), and as the "flowers of tan" are often found in summer on moist tan bark. If exposed to desiccation, the plasmodia of this Myxomycete pass into a resting state, and become converted into spherical or strand-like SCLEROTIA, from which a plasmodium is again produced on a further supply of water. Finally, the whole plasmodium becomes transformed into a dry cushion- or cake-shaped fructification of a white, yellowish, or brown colour. The fructification, in this instance, is enveloped by an outer calcareous crust or rind, and is subdivided by numerous internal septa. It encloses numerous dark violet-coloured spores, and is traversed by a filamentous capillitium, in which are dispersed irregularly-shaped vesicles containing granules of calcium carbonate. A fructification of this nature, or so-called æthalium, consists, therefore, of a number of sporangia combined together, while in most of the Myxomycetes the sporangia are simple and formed singly.

FIG. 225.—*Leocarpus fragilis.* Groups of sporangia upon Moss. (Nat. size.)

FIG. 224.—*Trichia varia.* *A*, Closed and open sporangia (× 6); *B*, a fibre of the capillitium (× 240); *C*, spores (× 240).

The structure and nature of the sporangia afford the most convenient means of distinguishing the different genera. The usually brown or yellow sporangia are spherical, oval, or cylindrical, stalked (Figs. 223, 225) or not stalked (Fig. 224). They usually open by the rupture of the upper portion of the sporangium walls, the lower portion persisting as a cup (Figs. 223, *B*, 224, *A*). In *Cribraria* (Fig. 223, *C*) the upper part of the wall of the sporangium, which contains no capillitium, becomes perforated in a sieve-like manner. In *Stemonitis* (Fig. 223, *A*) the whole peridium falls to pieces, and the capillitium is attached to a collumella, which forms a continuation of the stalk.

Plasmodiophora Brassicae (⁵), one of the few parasitic Myxomycetes, causes tuberous swellings on the lateral roots of various species of *Brassica*. Its multinucleate Myxamœbæ occur in numbers in the cells of the hypertrophied parenchyma of these swellings; after the contents of the host-cell have been exhausted, they fuse into plasmodia, and these, eventually dividing into numerous spores, are set free by the disorganisation of the plant. The spores germinate like those of *Chondrioderma*, and the Myxamœbæ penetrate the roots of a young Cabbage-plant. The formation of true sporangia, however, does not take place, and this Slime-Fungus represents a more simply organised or, in consequence of its parasitic mode of life, a degenerate Myxomycete.

CLASS III

Bacteria (6)

Bacteria are unicellular or filamentous organisms of very simple construction. As a rule, chlorophyll is wanting in them, as in the *Myxomycetes*, and their mode of life is consequently a parasitic or saprophytic one. A large number of species exist distributed over the whole earth, in water, in the soil, in the atmosphere, or in the bodies of dead or living plants and animals. They are often termed Fission-Fungi, or *Schizomycetes*, since the multiplication of the unicellular forms takes place by a division into two and the separation of the segments. This mode of multiplication is, however, found in other unicellular plants.

The cells of the *Bacteria* are surrounded by a thin membrane, and contain a protoplasmic body, which is usually colourless, and can be made to contract away from the membrane by plasmolysis. The protoplasm may contain one or more vacuoles. One or several granular structures are also present in the protoplast; these so-called chromatin bodies may be deeply coloured by stains, and have been regarded as nuclei by various authors. Since, as yet, undoubted karyokinetic division has not been observed in these bodies, the presence of nuclei in the bacterial cell cannot be regarded as certainly established.

For the most part the *Bacteria* are extraordinarily minute organisms, and probably include the smallest known living beings. The spherical cells of the smallest forms of *Micrococcus* are only 0·0005 mm. in diameter; the rod-shaped cells of the tubercle bacillus are only 0·002-0·004 mm. long, while the transverse diameter of most species is about 0·001 mm.

The simplest form of Fission-Fungi are represented by minute spherical cells, COCCI. Forms consisting of rod-shaped cells are designated BACTERIUM or BACILLUS. Simple cell filaments are termed LEPTOTHRIX; spiral, closely-wound filaments are classified as SPIRILLUM, when more loosely wound as VIBRIO, and longer spiral filaments as SPIROCHÆTE. In the highest stage of their development the Fission-Fungi consist of cell filaments exhibiting false branching. The unicellular cocci, rod-shaped forms, and vibrios may also remain united in chains after the cell-division. Frequently the cell-membranes undergo a mucilaginous swelling, the cells or cell-rows being embedded in the gelatinous mass. This stage of development is termed ZOOGLŒA.

Many Bacteria are motile. Their independent movements are due to the vibration and contraction of fine protoplasmic cilia. These flagella, according to A. FISCHER, are either distributed over the whole surface of the cells (peritrichous) (*e.g. Bacillus subtilis*, Fig. 228, *a*, *d*; *Typhus bacillus*, 226, *c*; *Tetanus bacillus*, 231, *e*), or they are polar, and spring from a single point either as a single flagellum (monotrichous) or as a group (lophotrichous). A single, polar flagellum occurs in *Vibrio cholerae* (Fig. 226, *a*); a polar terminal tuft of flagella in *Spirillum undula* (Fig. 226, *b*, *d*); a lateral polar tuft in the swarm-spores of *Cladothrix* (Fig. 227). The ciliary tufts may become so closely intertwined as to present the appearance of a single thick flagellum. The cilia, although arising from a protrusion of the cell protoplasm, are never drawn within the body of the cell, but undergo dissolution before the formation of spores takes place, or under unfavourable conditions (Fig. 226, *e*).

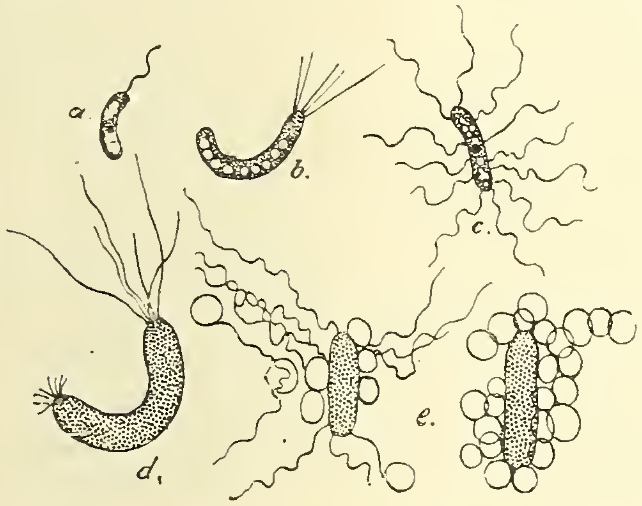


FIG. 226.—Types of arrangement of flagella. *a*, *Vibrio cholerae*; *b*, *d*, *Spirillum undula*; *d*, development of a new bunch of cilia in division; *c*, *Bacillus typhi*; *e*, *Bacillus subtilis*. (After A. FISCHER, × 2250.)

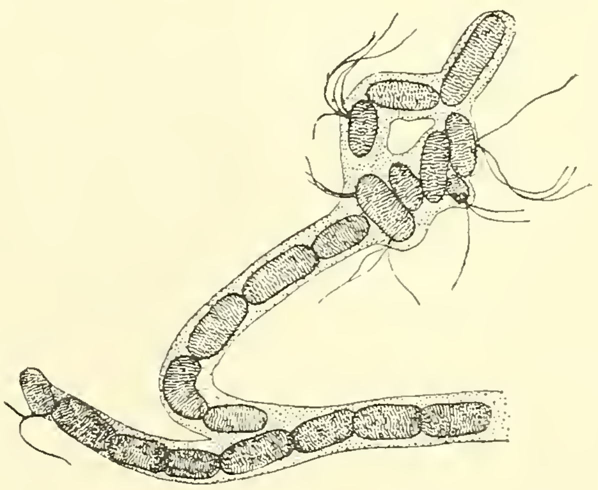


FIG. 227.—*Cladothrix dichotoma*. Formatio of swarm cells from the cells of the filament. (After A. FISCHER, × 1000.)

Multiplication of the individual is accomplished vegetatively by the active division or fission of the cells; the preservation and distribution of the species by the asexual formation of resting spores. These arise as endospores (Figs. 228, *c*; 230, *e*, *f*) in the middle or at one end of a cell by the inner portion of the protoplasm separating itself from the peripheral, and surrounding itself with a thick membrane. The membrane of the mother cell becomes swollen and disintegrated when the spore is ripe. Spores are not found in all species.

Bacillus subtilis, the Hay bacillus (Fig. 228), which appears as a rule in the decoction obtained by boiling hay in water, will afford an example of the life-history of a Bacterium. The spores of this species, which withstand the effect of the boiling water, produce on germination rod-shaped swarming cells with cilia on all sides; these divide and may remain connected in short chains. At the surface of the fluid these swarming cells change into non-motile cells without cilia, which divide up, giving rise to long intertwined chains of cells. These are associated together in the pellicle covering the surface (zoogloea stage). Spore formation occurs when the nutritive substances in the fluid are exhausted.

Although the cycle of forms passed through in the life-history of a Bacterium is a very simple one, the individual species, which can often be barely distinguished by morphological characters, show great variety in their metabolic processes and in their mode of nutrition. The majority of Bacteria require oxygen for their respiration, and are therefore aerobic; many can, however, develop without this gas, while some species, *e.g.* the butyric acid bacterium and the tetanus bacillus, are strictly anaerobic and only succeed in the absence of oxygen (cf. p. 219).

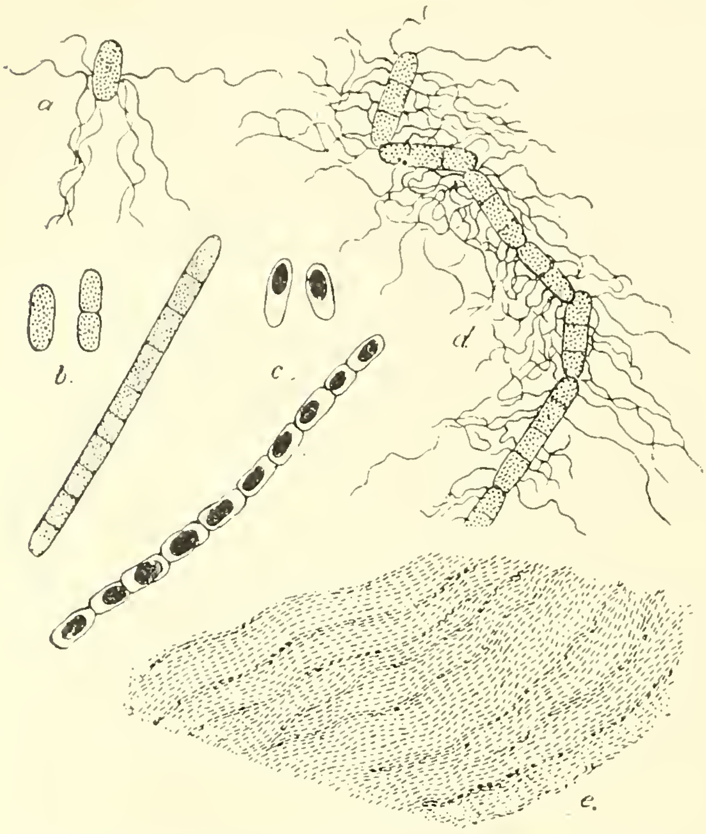


FIG. 228.—*Bacillus subtilis.* *a*, *d*, Motile cells and chain of cells; *b*, non-motile cells and chains of cells; *c*, spores from the zoogloea, *e*. (From A. FISCHER, Vorles. über Bacterien. *a*-*d*, × 1500; *e*, × 250.)

Saprophytic and parasitic species are distinguished, though a sharp separation is often impossible. In cultures the parasitic forms can be made to lead a saprophytic life on suitable substrata.

To the saprophytic Bacteria belong in the first place the forms which inhabit water. The widely distributed *Cladothrix dichotoma* is morphologically the highest among these. It is found in stagnant water, and consists of falsely branching, delicate filaments attached to Algæ, stones, and woodwork, and forming a slimy coating over them; the filaments are composed of rod-shaped cells. Reproduction is effected by ciliated swarm-cells, which originate by division from cells of the filament and are set free by the swelling of the sheath (Fig. 227). The swarm-cells come to rest after a time and grow into new filaments.

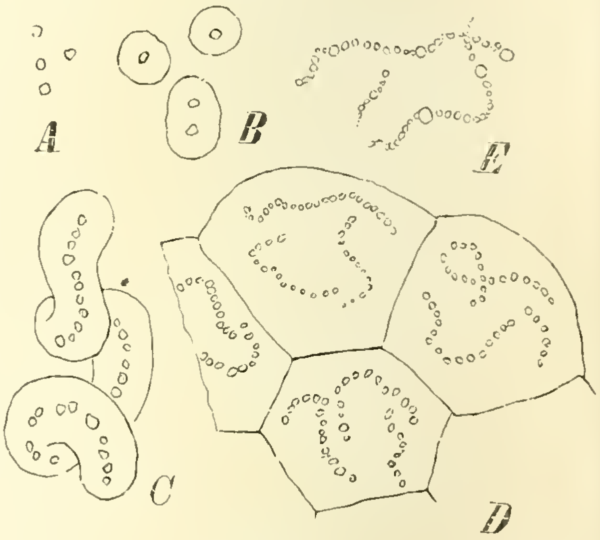


FIG. 229.—*Leuconostoc mesenterioides.* *A*, Isolated spores; *B*, *C*, formation of chain of cells with gelatinous sheath; *D*, portion of mature zoogloea; *E*, formation of spores in the filaments of the zoogloea. (After VAN TIEGHEM, × 520.)

Another very common form is *Crenothrix Kühniana,* which consists of unbranched filaments attached to the substratum, but easily broken. It often forms masses in the cavities of water-pipes, blocking them up and rendering the water undrinkable. The reproduction of *Crenothrix* is effected by small, round, non-motile cells, which arise by subdivision of the cells of a filament enclosed by its sheath.

The numerous kinds of Sulphur Bacteria, of which the filamentous *Beggiatoa alba* is the most widely distributed, are found in sulphurous springs and at the bottom of pools where sulphuretted hydrogen is being formed by decomposition of organic material. These Bacteria oxidise sulphuretted hydrogen into sulphur, and store the latter substance in the form of rounded granules within their cells.

Leptothrix ochracea, the so-called Iron Bacterium, oxidises oxide of iron to the hydrated oxide of iron, which it accumulates in the sheaths of its filaments.

The zymogenous or fermentation Bacteria and the saprogenous or decomposition Bacteria are other saprophytic forms. The former oxidise or ferment carbohydrates. The latter decompose nitrogenous animal or vegetable substances (albumen, meat, etc.) with the liberation of ill-smelling gases.

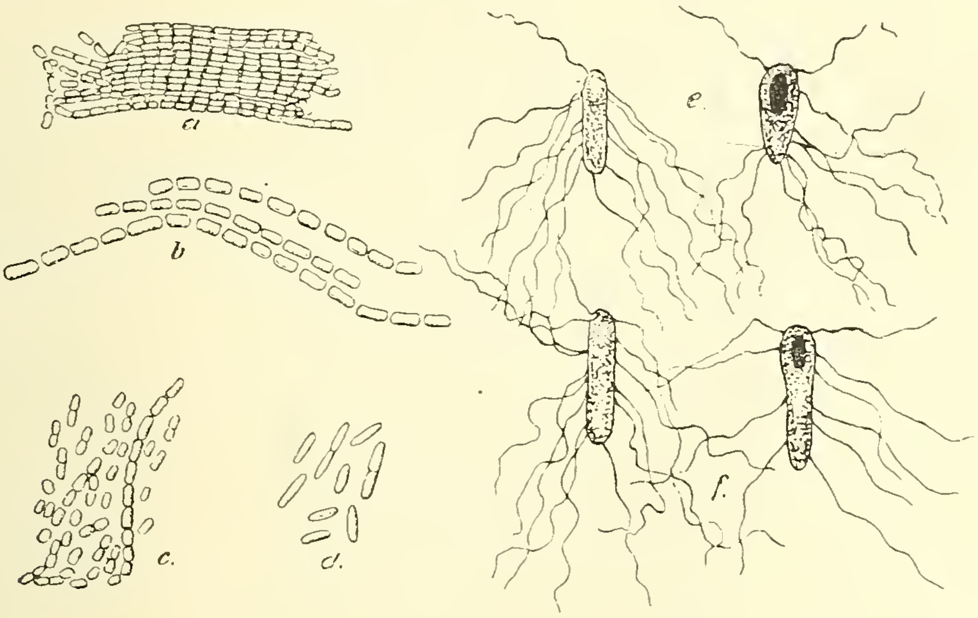


FIG. 230.—Bacteria of fermentation. *a-c*, Vinegar bacteria ; *a*, *Bacillus aceti ;* *b*, *Bac. Pasteurianus ;* *c*, *Bac. Kutzigianus ;* *d*, *Bac. acidi lactici*, lactic acid bacillus ; *e*, *Clostridium butyricum*, butyric acid bacillus ; *f*, *Plectridium paludosum*, fermentation bacterium from marsh water. (From A. FISCHER, Vorles. über Bacterien, × 1000.)

Thus *Leuconostoc mesenterioides* (Fig. 229) causes fermentation of beet-sugar. It forms large mucilaginous masses like frog-spawn, the bead-like rows of cells being surrounded by a gelatinous investment. The acetic acid Bacteria (Fig. 230, *a*, *b*, *c*) oxidise alcohol to acetic acid. The transformation of sugar into lactic acid is brought about by the rod-like cells of *Bacillus acidi lactici* (Fig. 230, *d*), *Clostridium butyricum* (Fig. 230, *e*) forms butyric acid from various carbohydrates in the absence of oxygen, while certain marsh Bacteria (Fig. 230, *f*) in the absence

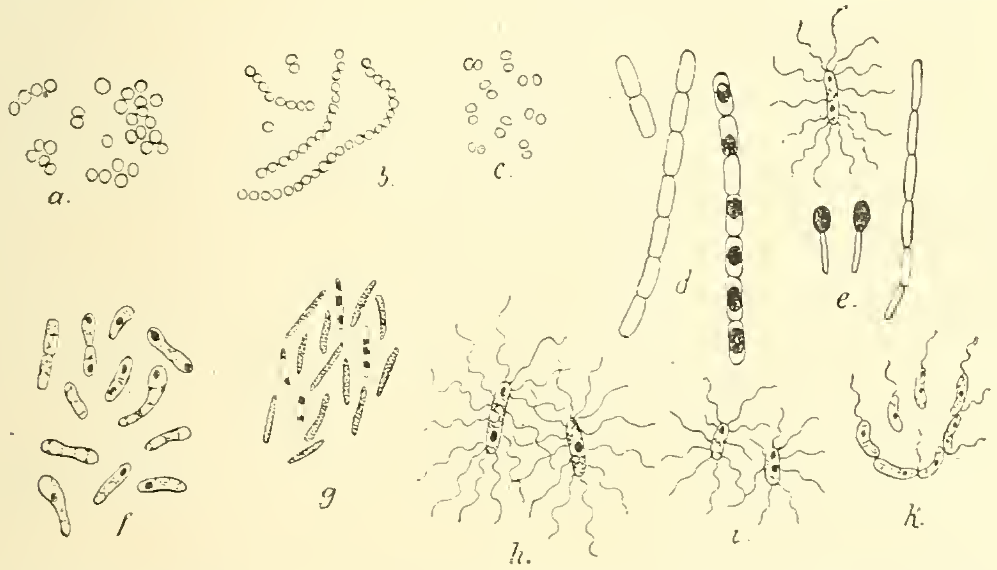


FIG. 231.—Pathogenic Bacteria. *a*, Pus cocci ; *b*, erysipelas cocci ; *c*, gonorrhea cocci ; *d*, splenic fever bacilli ; *e*, tetanus bacilli ; *f*, diphtheria bacilli ; *g*, tubercle bacilli ; *h*, typhoid bacilli ; *i*, colon bacilli ; *k*, cholera bacilli. (From A. FISCHER, Vorles. über Bacterien, × about 1500.)

of oxygen form marsh-gas from cellulose. *Bacillus vulgaris* is the most common cause of decomposition of meat, albumen, etc.

The numerous pathogenic Bacteria are the most important causes of infectious diseases. Their injurious influence on the tissues and blood of men and animals is brought about by the excretion of poisonous substances, to which the name toxins has been given. The following forms may be mentioned. *Staphylococcus pyogenes* (Fig. 231, *a*), the cocci of which form irregular or racemose masses, is the most common cause of suppuration, while *Streptococcus pyogenes* (Fig. 231, *b*), with cocci united in chains, occurs in erysipelas and other suppurative lesions. *Micrococcus* (*Diploeoccus*) *Gonorrhocae* (Figs. 231, *c*, 232, *a*) has somewhat flattened cocci arranged in pairs, and causes gonorrhoea. *Bacillus anthracis* (Figs. 231, *d*, 232, *c*) was found by R. KOCH in the blood and organs of animals suffering from splenic fever. The relatively large rod-shaped cells may be united in short chains; they form endospores in cultures in the same way as the Hay bacillus.

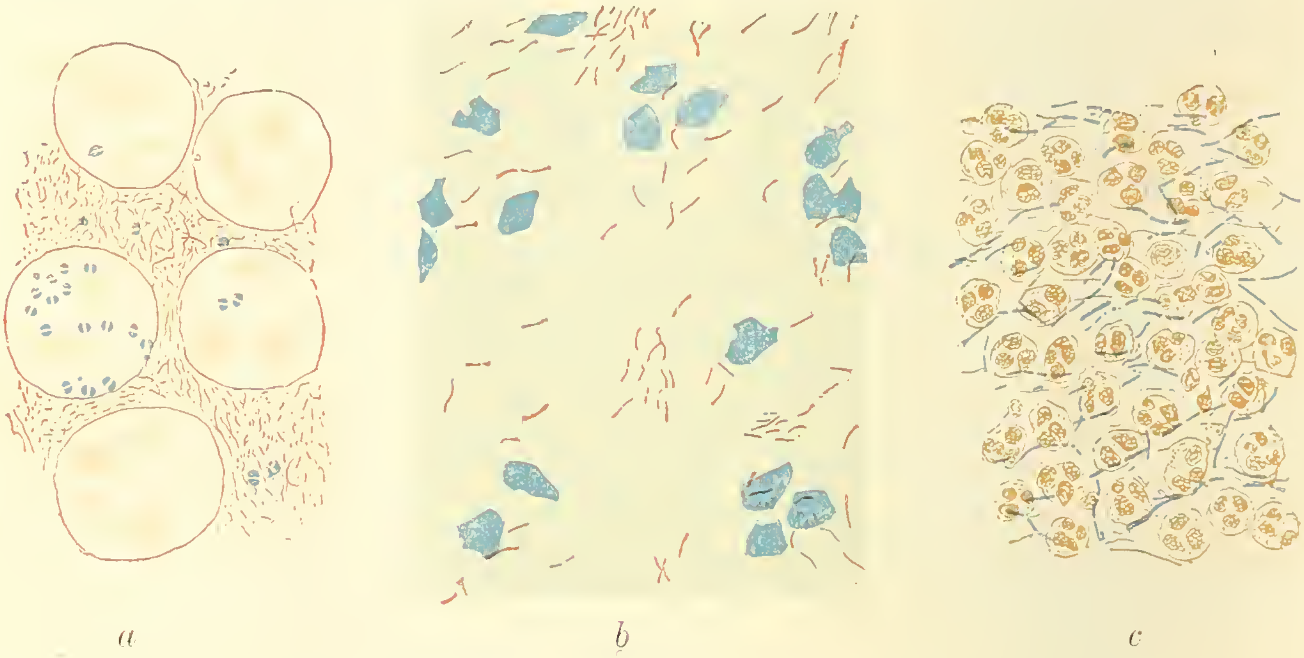


FIG. 232.—Stained preparations from Ziegler's *Text-book of Pathology*. *a*, gonococci in the gonorrheal discharge, mucus and pus corpuscles with cocci (methylene blue and eosin), × 700; *b*, tubercle bacilli in sputum of phthisis (fuchsin and methylene blue), × 400; *c*, splenic fever bacilli in the pustule of the disease (methylene blue and vesuvin), × 350. (From A. FISCHER, Vorles. über Bacterien.)

Bacillus tetani (Fig. 231, *e*) occurs in the soil, and is the cause of tetanus. Its straight rod-shaped cells are ciliated, and grow only in the wound itself; their spores are formed in the swollen end. LÖFFLER'S *Bacillus Diphtheriae* (Fig. 231, *f*) consists of small rod-shaped cells sometimes thickened at one end. KOCH'S *Bacillus tuberculosis* (Figs. 231, *g*, 232, *b*), which is found in all tuberculous lesions and secretions, as in the sputum, is a slender, slightly curved rod. Typhoid fever is caused by the ciliated cells of *Bacillus typhi* (Fig. 231, *h*); *Bacillus coli* (Fig. 231, *i*), the colon bacillus, which is as a rule harmless and always occurs in the human intestine, closely resembles the typhoid bacillus. The comma bacillus of Asiatic cholera, *Vibrio cholerae* (Fig. 231, *k*), was discovered by R. KOCH. It occurs in the intestine as short curved rods with a single polar flagellum, and sometimes in longer chains of spirally wound cells. *Spirochaete obermeieri*, which consists of long, thin, spirally wound filaments, without flagella, but capable of motion, occurs in the blood during the attacks of relapsing fever, of which it is the cause.

Besides the above injurious parasites there are others which are more or less harmless occurring on the mucous membranes, in the mouth (Fig. 4), or the intestine. *Sarcina ventriculi*, which occurs as packets of cocci in the stomach and intestine of man, will serve as an example of these.

The Bacteria included under the name *Bacillus radicicola* (=Rhizobium Leguminosarum) occur in the root-tubercles of *Leguminosae*, and, like certain other Bacteria found in the soil, are capable of utilising free nitrogen in their metabolism (p. 210).

In addition to saprophytic and parasitic Bacteria there are some which, though possessing no chlorophyll, obtain their food from inorganic compounds only. These are the nitrite Bacteria (*Nitrosomonas*) and the nitrate Bacteria (*Nitrobacter*), which live in the soil. They oxidise ammonia to nitrous, and this to nitric acid, and obtain their carbon from carbonic acid; they thus derive their food independently of any organic food-supply (Fig. 233, cf. p. 197).

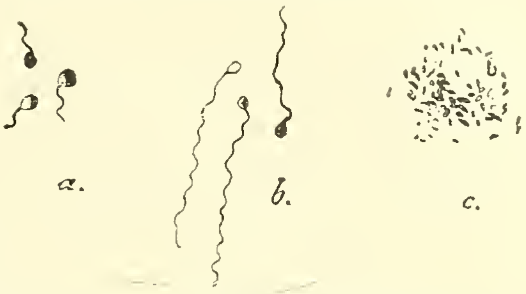


FIG. 233.—Nitrifying bacteria, after Winogradsky. *a*, *Nitrosomonas europaea*, from Zurich; *b*, *Nitrosomonas javanensis*, from Java; *c*, *Nitrobacter*, from Queto. (From FISCHER, Vorles. über Bacterien, × 1000.)

CLASS IV

Cyanophyceae, Blue-green Algæ (7)

The *Cyanophyceae* are simply organised unicellular or filamentous Thallophytes of a bluish-green colour; the cells or filaments are frequently united into colonies by the gelatinous swelling of the cell walls. The numerous species, which are distributed over the earth,

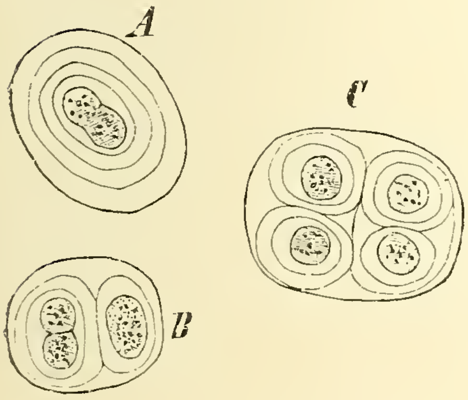


FIG. 234.—*Gloeocapsa polydermatica*. *A*, In process of division; *B*, to the left, shortly after division; *C*, a later stage. (× 540.)

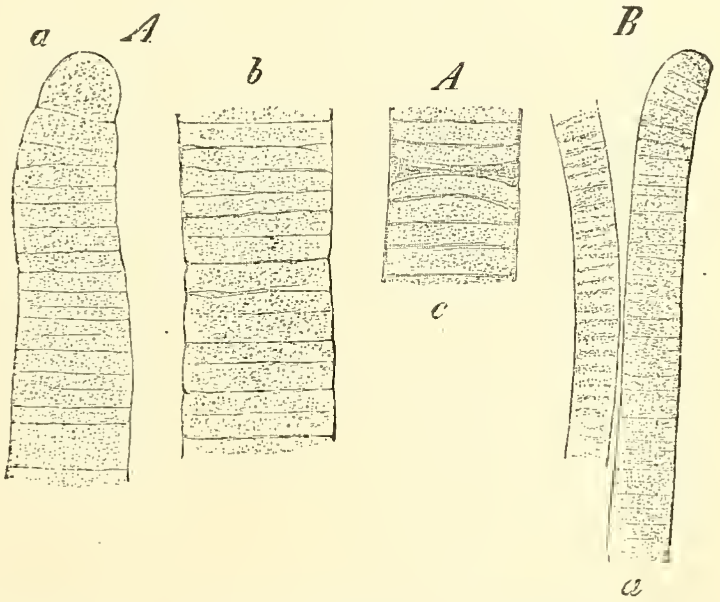


FIG. 235.—*A*, *Oscillaria princeps*; *a*, terminal cell; *b*, *c*, portions from the middle of a filament. In *c*, a dead cell is shown between the living cells. *B*, *Oscillaria Froelichii*. (× 540.)

live in water, or form gelatinous or filamentous growths on damp soil, damp rocks, or the bark of trees.

The type of protoplast enclosed by the cell wall differs in several respects from that of other Algæ. A peripheral zone can be distinguished which has the functions of a chromatophore; chlorophyll, together with a blue-green pigment, phycocyan, after which the group is named, are contained in this layer. The colourless central body enclosed by the coloured zone perhaps corresponds to a nucleus, though as yet the characteristic structure and mode of division of a nucleus have not been demonstrated with certainty. Granules occurring in the cells, especially in the peripheral zone (cyanophycin granules, central granules), probably are of the nature of reserve substances.

Reproduction is exclusively vegetative by cell division. In many forms resting spores are formed by the enlargement of single cells, the walls of which become greatly thickened (Fig. 236).

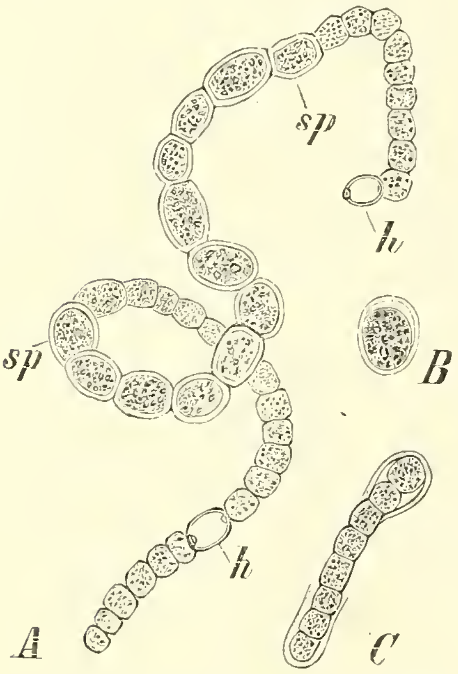


Fig. 236.—*Nostoc Linckii.* *A*, Filament with two heterocysts (*h*) and a large number of spores (*sp*); *B*, isolated spore beginning to germinate; *C*, young filament developed from spore. (After Bornet, × 650.)

Just as the Bacteria are designated Fission-Fungi (*Schizomycetes*), the Blue-green Algæ may be termed Fission-Algæ (*Schizophyceae*), since the reproduction of both depends on fission. The two groups would form the class of fission plants *Schizophyta*. The origin of *Bacteria* from the *Cyanophyceae* is still, however, open to doubt, since the cilia and endospores of the former are unknown in the latter group.

The simplest *Cyanophyceae* consist of spherical cells; this is the case with species of *Chroococcus*. In *Gloeocapsa* (Fig. 234), found on damp rocks and walls, the cells remain connected together after division into a gelatinous mass, forming a multicellular colony.

The species of *Oscillaria*, which occur everywhere in water or on damp soil, are the simplest of the filamentous forms. The filament, which is usually provided by a thick sheath, consists of similar flattened cells (Fig. 235). It can separate into pieces (hormogonia), which become free owing to the pressure of the sheath, and grow into new filaments.

In other filamentous *Cyanophyceae* specially modified cells with degenerated contents occur in the filament. The significance of these heterocysts is not yet clear. The species of *Nostoc* (Fig. 236), whose bead-like filaments are united into more or less spherical gelatinous colonies living on damp soil or in water, afford an example of this.

Many *Cyanophyceae* take part with the Fungi in the formation of Lichens. Some species also are endophytic and inhabit cavities in other plants, *e.g. Anabaena* in *Azolla*, *Nostoc* in some Liverworts, in *Lemna*, and in the roots of *Cycas* and *Gunnera*.

CLASS V

Diatomeae (Diatoms) (8)

The *Diatomeae* constitute a very large class of unicellular Algæ. They usually occur associated together in large numbers, in both fresh and salt water, and also on damp soil.

The individual cells are either solitary and free-swimming, or they are attached by means of gelatinous stalks, excreted by the cells themselves (Fig. 237). Sometimes these chains remain connected and form bands or zigzag chains, or, on the other hand, they are attached and enclosed in gelatinous tubes, while in the case of the marine genus *Schizonema* they lie embedded in large numbers in a gelatinous branching thallus, often over 1 dcm. in breadth. The cells also display a great diversity of shape; while generally bilaterally symmetrical, they may be circular or elliptical, rod- or wedge-shaped, curved or straight. The structure of their cell walls is especially characteristic; it is composed of two halves or VALVES, one of which overlaps the other like the lid of a box (Fig. 3, *B*). The cells thus present two altogether different views, according to the position in which they are observed, whether from the GIRDLE (Fig. 3, *B*) or VALVE-SIDE (Fig. 3, *A*). Both valves are so strongly impregnated with silica, that, even when subjected to intense heat, they remain as a siliceous skeleton, retaining the original form and markings of the cell walls. The walls of the cells, particularly on the valve side, are often ornamented with numerous fine, transverse markings or ribs, and also with small protuberances and cavities, or they are perforated by open pores. In many instances (Fig. 3) a longitudinal line corresponding to an opening in the cell walls, and exhibiting swollen nodules at both extremities and in the middle, is distinguishable in the surface of the valves. Forms provided with such a median suture or RAPHE are characterised by peculiar backward-creeping movements, resulting from the extrusion of

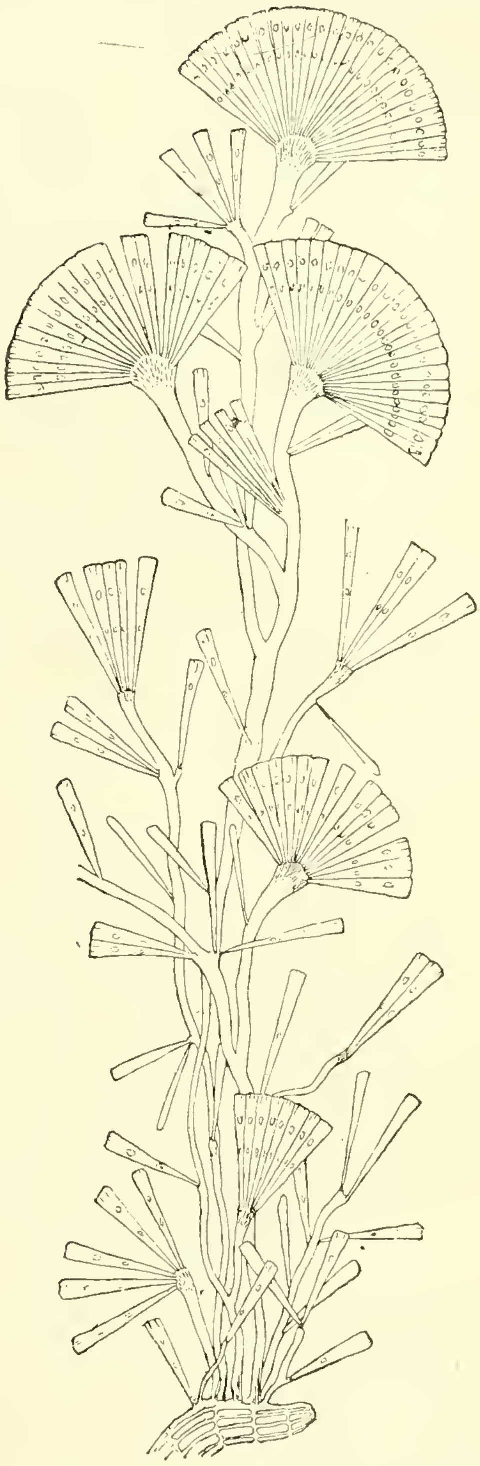


FIG. 237.—*Licmophora flabellata.* Colony of Diatoms with branched gelatinous stalks. (After SMITH, from Goebel's *Organographie.*)

protoplasmic protrusions from their longitudinal edges (cf. p. 242). Each frustule has always a central nucleus and one (Fig. 3) or two large, or numerous smaller chromatophores embedded in its parietal protoplasm. These chromatophores or ENDOCHROME PLATES, as they are often called, are flat, frequently lobed, and of a brownish-yellow colour. In addition to chlorophyll they contain a golden brown colouring matter, termed DIATOMIN. Globules of a fatty oil are also included in the cell contents, and take the place of starch as an assimilation product.

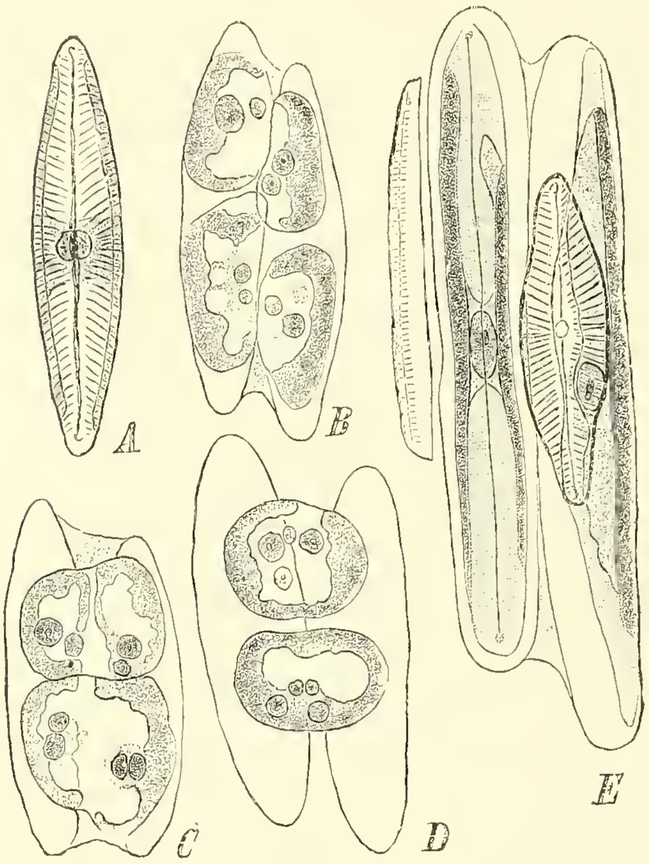


FIG. 238.—Formation of auxospores in *Navicula viridula*. *A*, Cell seen from the valve side. *B*, Two cells lying alongside one another; their contents have divided into two daughter cells, each of which possesses two nuclei. *C*, *D*, Conjugation in pairs of the daughter cells to form the auxospores, which at first contain four nuclei. *E*, The two full-grown auxospores; the two larger nuclei in each have fused into one, the two smaller ones have disintegrated. (After KARSTEN, × 500.)

The *Diatomeae* multiply vegetatively by bipartition, which always takes place in one direction. In this process the two valves are first pushed apart from one another by the increasing protoplasmic contents of the mother cell, which then divides longitudinally and always in such a direction that each of the two new cells retains one valve of the mother cell. After the division of the protoplasm of the mother cell is accomplished, each daughter cell forms, on its naked side, a new valve fitting into the old one. The two valves of a cell are therefore of different ages. In consequence of this peculiar manner of division, as the walls of the cells are silicified and incapable of distension, the daughter cells become successively smaller and smaller, until finally, after becoming reduced to a definite minimum size, they undergo transformation into AUXOSPORES. The auxospores are usually two or three times larger than the cells from which they arise, and by their further development they re-establish the original size of the cells.

The formation of auxospores is accomplished in various ways. According to G. KARSTEN four main types can be distinguished, which can all be derived from the original type of *Rhabdonema arcuatum*. In this species the contents of the mother cell divide into two daughter cells, which escape from the siliceous cell wall and grow into the auxospores; the latter are two to three times the size of the mother cell. The second type (Fig. 238) occurs in many *Diatomaceae*; in this two cells lay themselves side by side, and their contents divide into daughter cells; these round themselves off, emerge from the cell wall, and give rise to the auxospores by conjugation. In the third type (*Cocconeis*) a single auxospore is formed as the result of conjugation of the contents of the two parent cells. In the fourth type (*Melosira*) an auxospore arises from the mother cell directly, without previous conjugation. A suppressed process of division can be detected in the last case, however, and it seems probable that a preliminary cell-division is an original characteristic of all methods of producing auxospores.

Countless numbers of Diatoms live in the ocean, and they constitute also a proportionately large part of the PLANKTON (9), that is, the free-swimming organic world on the surface of the sea. The plankton Diatoms have no middle suture or raphe on the surface of their valves, and are especially adapted to swimming or floating. To this end they are often provided with horn-like protuberances or membranous wings, which, like the contrivances of seeds for a similar purpose, greatly enhance their buoyancy.

Many Diatoms occur in places when decomposing substances are present in abundance. Such species can assume a saprophytic mode of life, their chromatophores becoming colourless and reduced in size. It has been shown that some colourless species of *Nitzschia* which occur in the sea are exclusively dependent on organic substances for food, the reduction of their chromatophores being complete (10).

Diatoms occur also as fossils. Their silicified valves form a large part of the deposits of SILICEOUS EARTH, Kieselguhr, mountain meal, etc., and in this form they are utilised in the manufacture of dynamite.

On account of the extreme fineness of the markings of their valves, it is customary to employ certain species of Diatoms as test objects for trying the lenses of microscopes. *Pleurosigma angulatum* is commonly used for this purpose, and, with a sufficiently strong lens, it is possible to distinguish on the surface of the S-shaped valves a system of fine markings, forming a network of six-sided meshes to the right and left of the raphe.

CLASS VI

Peridineae (9-11)

The *Peridineae* live for the most part in salt water, and form, together with the *Diatomeae*, an important part of the plankton floating on the surface of the ocean. Their cell plasma contains a nucleus, a complicated system of vacuoles, and light yellow, tabular chromatophores. The *Peridineae* are further characterised by two long protoplasmic cilia or flagella, to the vibrations of which the movements of the cells are due. The flagella spring from the ventral side of the cells, and lie in two furrows, which cross each other at right angles, on their surface (Fig. 239). Only a few *Peridineae* are entirely naked; most of them have peculiarly sculptured cell walls, consisting of intersecting cellulose plates or ribs. They multiply by division, and in the autumn form thick-walled cysts, in which condition they pass the winter. Conjugation has not been observed.

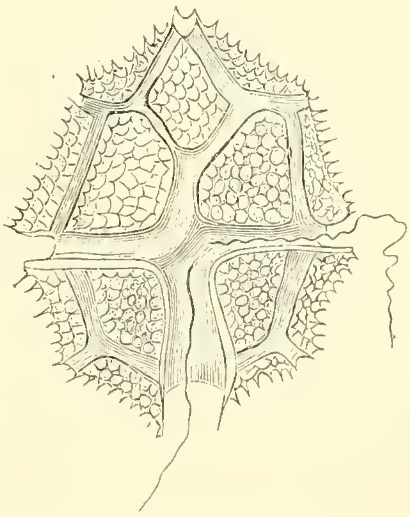


FIG. 239.—*Peridinium bipes*, ventral view. (After SCHILLING, × 750.)

In addition to the forms which, like Algæ, sustain themselves by means of assimilating yellow chromatophores, there occur also colourless *Peridineae*, whose chromatophores are only represented by colourless leucoplasts. Such species, although nearly related to the brown *Peridineae*, live either as saprophytes or in the same way as animals. *Gymnodinium hyalinum*, a colourless, naked, fresh-water form, exhibits a mode of life resembling that of a Myxomycete. For the purpose of absorbing nourishment it loses its cilia and assumes the form of an amœba; in this condition it encloses and digests small Algæ.

CLASS VII

Conjugatae (12)

In the class of the *Conjugatae* is included a large independent group of green, fresh-water Algæ, in the form either of solitary cells or filamentous rows of cells. They derive their name from their peculiar mode of sexual reproduction, which consists in the CONJUGATION of two apparently similar cells, resulting in the formation of a ZYGOSPORE. They are in this respect sharply distinguished from all the other green Algæ, the *Chlorophyceae*, from which they may be distinguished also by the absence of any asexual mode of spore-formation, and by the complicated structure of their green chromatophores. The unicellular forms present some similarities to the Diatoms.

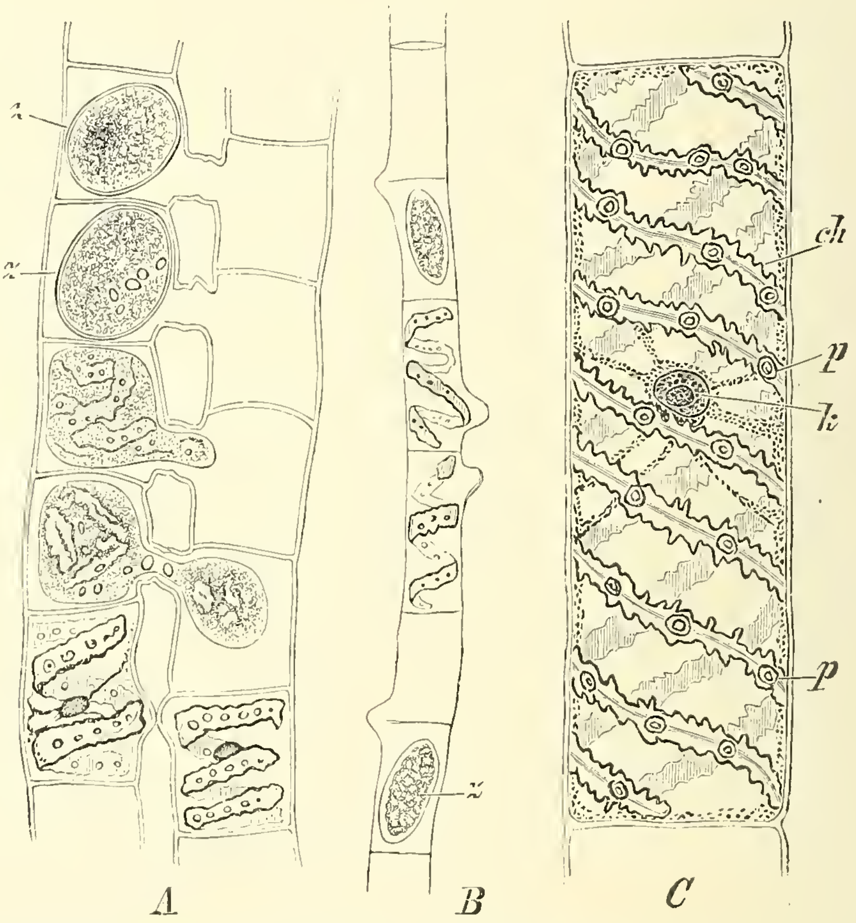


FIG. 240.—*A*, Conjugation of *Spirogyra quinina* (× 240). *B*, *Spirogyra longata* (× 150); *z*, zygospore *C*, Cell of *Spirogyra jugalis*; *k*, nucleus; *ch*, chromatophores; *p*, pyrenoid. (× 256.)

1. In the DESMIDIACEAE are comprised the unicellular forms. They are ornamented with delicate markings, and, like the Diatoms, exhibit a great variety of form (Figs. 241, 242). Their cells are composed of two symmetrical halves, separated, as a rule, from each other by a deep constriction, the isthmus. Each half contains a large, radiate, irregularly defined chromatophore, or a number of plate-like chromatophores united into one. Within the chromatophores are disposed several pyrenoids, while the nucleus lies in the centre of the cell in the constriction. The cells themselves display a great diversity of form and external configuration (Figs. 241, 242). The cell walls are frequently beset with wart- or horn-like protuberances. In some genera there is no constriction between the two halves of the cell. This is the case, for instance, in the crescent-shaped *Closterium moniliferum* (Fig. 242), whose two chromatophores consist of six elongated plates, united in the long axis of the plant, while in each end of the cell there is a small vacuole containing minute crystals of gypsum in constant motion. Many Desmids are characterised by heliotactic movements; they protrude fine mucilaginous threads through the cell walls, by means of which they can push themselves along, and take up a position in a line with the direction of the incident rays of light.

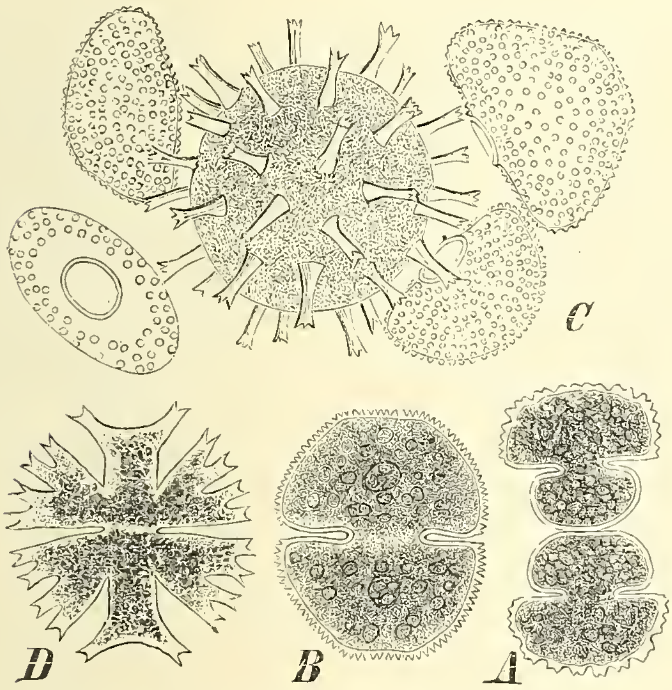


FIG. 241.—*A*, *Cosmarium coelatum* in process of division; *B*, *Cosmarium Botrytis*; *C*, the same with fully-developed zygospore; *D*, *Micrasterias Crux melitensis*. (After RALFS.)

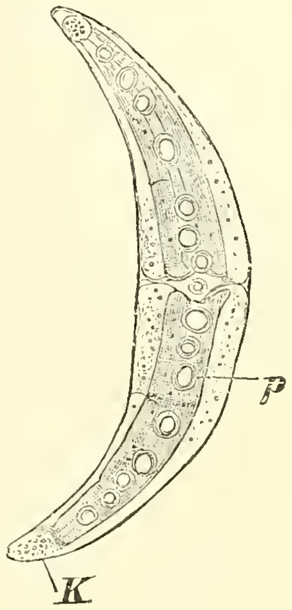


FIG. 242.—*Closterium moniliferum*; *p*, pyrenoid; *K*, vesicle with crystals. × 240.)

Multiplication is effected by cell division. This is accomplished by the formation of a partition wall across the middle of the cell after the nuclear division is completed. Each daughter cell eventually attains the size and form of the mother cell, by the outgrowth of a new half on the side towards the new division wall (Fig. 241, *A*). After the completion of their growth, the two cells separate from each other.

The conjugation of the protoplasts takes place, in the case of the *Desmidiaceae*, outside their cell walls. Two cells approach each other, and surround themselves with a mucilaginous envelope. Their cell walls rupture at the constriction, and parting in half allow the protoplasts to escape, which then unite to form a zygospore. The zygospores of the *Desmidiaceae* frequently present a very characteristic appearance, as their walls are often beset with spines (Fig. 241, *C*). The four empty cell halves may be seen close to the spore.

2. ZYGNEMACEAE.—In this family, all of which are filamentous in character, the genus *Spirogyra*, with its numerous species, is the best known. It is commonly found in standing water, forming unattached masses of intertangled green filaments. The filaments exhibit no distinction of base and apex, and are composed of simple rows of cells, which vary in length in different species. Growth results from the division and elongation of the cells in one direction only. Each cell has a large nucleus situated either in the peripheral protoplasm or suspended in the centre of the cell by protoplasmic threads extending from the parietal protoplasm. The name of the genus, *Spirogyra*, is due to the peculiar spiral form of its green band-like chromatophores (Fig. 240, *C*). The cells of *Zygnema* contain two star-shaped chromatophores.

CONJUGATION, in the case of *Spirogyra*, is preceded by the development of converging lateral processes from the cells of adjacent filaments. When two processes from opposite cells meet (Fig. 240, *A*), their walls become absorbed at the point of contact, and the whole protoplasmic contents of one cell, after contracting from the cell wall, passes through the canal which is thus formed into the opposite cell. The protoplasm and nuclei of the conjugating protoplasts then fuse together and form a zygospore invested with a thick wall, and filled with fatty substances and reddish-brown mucous globules. It is the function of the zygospore to act as a resting-spore, to tide over the winter or a period of drought, and eventually, on germination, to give rise to a new filament of *Spirogyra*. This form of conjugation, which is the one peculiar to most species, is described as scalariform (Fig. 240, *A*), as distinct from the lateral conjugation of some species, in which two adjacent cells of the same filament conjugate by the development of coalescing processes, which are formed near their transverse wall (Fig. 240, *B*).

CLASS VIII

Chlorophyceae (Green Algæ) ([13, 14])

In the *Chlorophyceae* are included the majority of the Algæ provided with green chromatophores. They group themselves naturally into three orders, according to the structure of the thallus: the *Protococcoideae*, which include all the unicellular forms, whether living as isolated cells or as cell colonies; the *Confervoideae*, comprising forms consisting of simple or branched cell filaments or cell surfaces; the *Siphoneae*, with a thallus variously developed, but usually consisting of a single, multinuclear, tubular cell.

Sexual reproduction has not been demonstrated for all species of the *Chlorophyceae*. In the simplest cases it is effected by the conjugation of naked gametes, of similar form and equal size. The gametes, as distinct from those of the *Conjugatae*, are motile ciliated protoplasts, and are known as PLANOGAMETES. In other genera there is a differentiation of the sexual cells into a female non-motile egg-cell or OOSPHERE and a motile ciliated male cell or SPERMATOZOID. Examples of this advance from ISOGAMY to OOGAMY are afforded by each of the above three orders.

In addition to sexual reproduction, the *Chlorophyceae* almost always exhibit an asexual mode of reproduction by the formation of motile ciliated SWARM-SPORES (ZOOSPORES) which resemble the planogametes.

The cells in which the swarm-spores are formed are termed SPORANGIA; similarly those producing gametes are designated GAMETANGIA. Cells in which spermatozoids take their origin are termed ANTHERIDIA; those giving rise to egg-cells, OOGONIA. If the sexual form be derived from an asexual form of reproduction, all these organs, as well as those similarly named in the other classes of the Thallophytes, must be regarded as homologous.

The *Conjugatae* and *Characeae*, as well as the three orders of the *Chlorophyceae*, also possess green chromatophores, and hence the designation Green Algæ, in its widest, unrestricted sense, is also applicable to them. The *Conjugatae*, however, are sharply characterised by their peculiar manner of sexual production. The *Characeae* also form a distinct group, and are marked off from the *Chlorophyceae* by the more highly advanced segmentation of their thallus and the more complicated structure of the female sexual organs and of the antheridia, both of which are enclosed within special enveloping receptacles, while the antheridia and oogonia of the *Chlorophyceae* are always devoid of any external covering of sheathing sterile cells.

Order 1. Protococcoideae (15)

The *Protococcoideae* include only unicellular Algæ, whose cells lead a separate existence, or are united into cell families with a definite or indefinite order of arrangement. They occur, for the most part, as freely-swimming, fresh-water forms, but are also found in damp places. The uninuclear cells have cell walls, and contain one or more chromatophores. In the simpler forms multiplication takes place vegetatively by cell division; but, in most cases, asexual swarm-spores, provided with two cilia, are produced. Sexual reproduction, which does not occur in all genera, is effected by the conjugation of two exactly similar planogametes which fuse into a zygospore or zygote. The fertilisation of an egg by a motile spermatozoid is only known to take place in the case of *Eudorina* and *Volvox*.

The simplest forms are spherical, free-living cells, which multiply by cell-division only. The genus *Chlorella* is particularly interesting from a biological standpoint also, as its small round cells live symbiotically in the plasma of *Infusoria*, in the cells of *Hydra viridis*, *Spongilla fluviatilis*, and other lower animals. The simplest type of cell-colony, consisting of four cells, is peculiar to the genus *Scenedesmus*. The commonest form, *Sc. acutus*, has spindle-shaped cells, while the colonies of *Sc. caudatus* are distinguished by four long horn-like prolongations of the cell wall (Fig. 243). In reproduction each cell divides in the direction of its length into four daughter cells, which, on escaping from the parent cell, form a new colony.

While *Scenedesmus* is reproduced by division only, *Pediastrum* (Fig. 244) may be cited as an example of a genus which gives rise to swarm-spores. Each cell-family forms a free-swimming plate, composed internally of polygonal cells, and on the margin it consists of cells more or less acutely crenated. The formation of asexual swarm-spores is effected in *Pediastrum* by the division of the contents of a cell into a number (in the case of the species illustrated, *P. granulatum*, into 16) of naked swarm-spores, each with two cilia. The swarm-spores, on escaping through the ruptured cell wall (Fig. 244, *A*, *b*), are enclosed in a common envelope. After first moving vigorously about within this envelope, they eventually collect together and form a new cell-family. *Pediastrum* possesses also a sexual mode of reproduction. The gametes are all of equal size, and except that they are smaller and are produced in greater numbers, they are otherwise similar to the swarm-spores. They move freely about in the water, and in conjugating fuse in pairs to form zygotes. The further development of the zygotes into cell-families is not yet fully known.

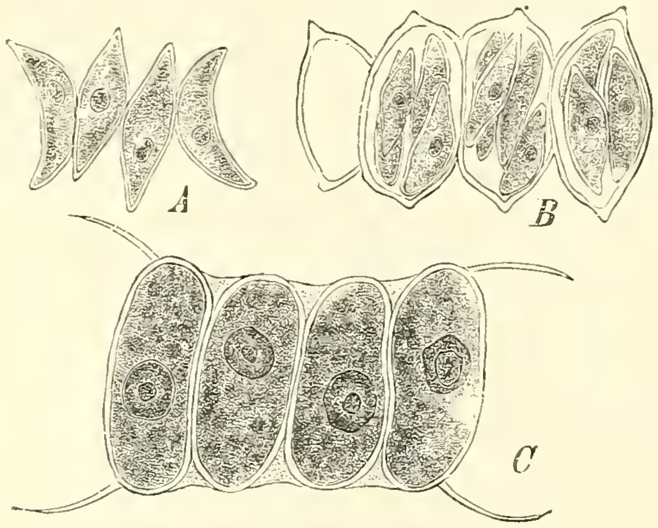


Fig. 243.—*A*, *Scenedesmus acutus*. *B*, the same, undergoing division; *C*, *Scenedesmus caudatus*. (After Senn, × 1000.)

The *Volvocaceae* include also forms whose cells live either isolated or united into colonies, but which, unlike the type of the *Protococcoideae* heretofore considered, are also provided in their vegetative state with cilia and surrounded by a delicate envelope. The cilia, usually two in number, project through this external envelope, and by means of them the Algæ of this family are enabled to swim freely about. In this respect they continue their vegetative existence in that condition which, in the case of the other *Protococcoideae*, is only assumed transitionally by the swarm-spores.

The genus *Sphaerella* (*Haematococcus*) belongs to the simplest solitary forms of this family; the presence of some forms of this (particularly *S. pluvialis*), on account of the hæmatochrome contained in their protoplasm, often impart a bright red colour to small pools of water in which they are found. *Sphaerella nivalis*, another species of this same genus, is also the cause of the so-called "red-snow" of the snowfields in high northern latitudes and in the Alps. The swarm-cells have a widely-distended envelope and two cilia (Fig. 245, *A*). Asexual multiplication is effected by the division of the cell into four motile swarm-spores (*B*); sexual reproduction by the conjugation of small biciliate gametes, of which 32-64 are produced by a cell, to form a thick-walled zygote (*C*-*G*).

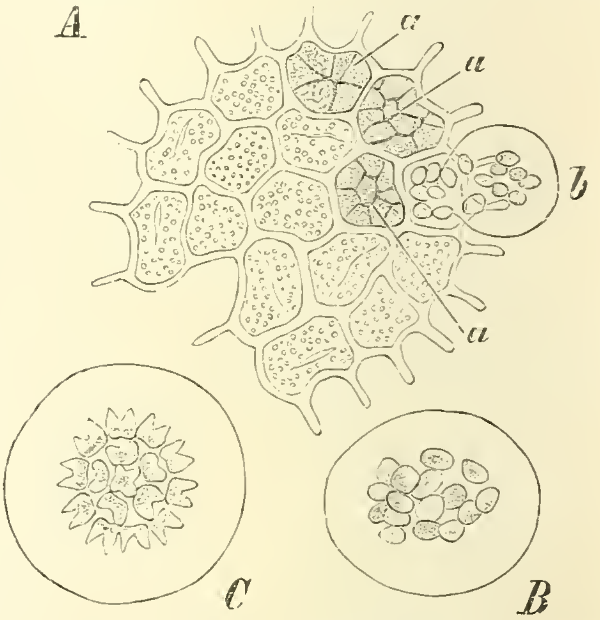


Fig. 244.—*Pediastrum granulatum*. *A*, An old cell-family: *a*, cells containing spores; *b*, spores in process of extrusion (the other cells have already discharged their spores); *B*, cell-family shortly after extrusion of the spores; *C*, cell-family 4½ hours later. (After Al. Braun, × 300.)

In *Volvox* (16), which may be regarded as the highest form in the order, the free-swimming colonies have the shape of a hollow sphere. The sexual cells are differentiated into ova and spermatozoids. The egg-cells arise by the enlargement of single cells of the colony; they are large, green, non-motile cells surrounded by a mucilaginous wall. The small spermatozoids are elongated bodies of a bright yellow colour, provided with two cilia at the colourless anterior end; they arise by the division of a cell of the colony into numerous daughter cells. After fusing with a spermatozoid within the cavity of the colony the egg-cell is transformed into the thick-walled, resting oospore.

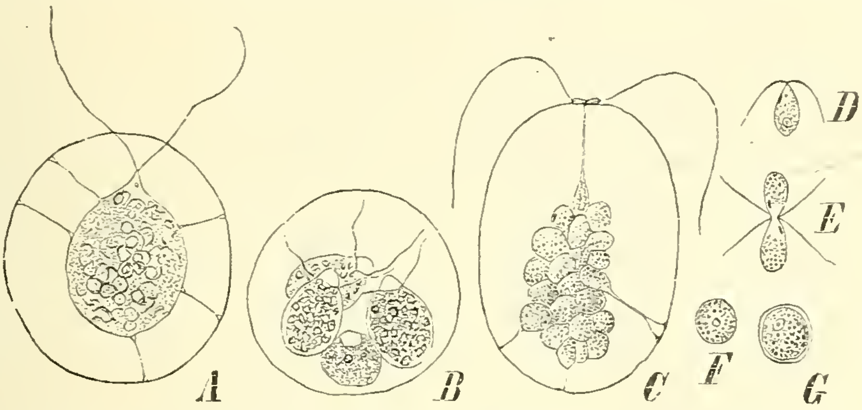


FIG. 245.—*A*, *B*, *Sphaerella pluvialis* (× 360): *A*, swarming cell; *B*, formation of swarm-spores. *C-G*, *Sphaerella Bütschlii*: *C*, formation of gametes (× 400); *D*, gamete; *E*, conjugation of two gametes; *F*, *G*, zygotes (× 800). (*C-G* after BLOCHMANN.)

Order 2. Confervoideae

The *Confervoideae* exhibit, as compared with the unicellular *Protococcoideae*, an advance in the external segmentation of the thallus. It is always multicellular, and, in most of the genera, consists of simple or branched filaments. The filaments are either attached by a colourless basal cell to the substratum or float free. The thallus of the marine genus *Ulva* (*Ulva lactuca*, SEA LETTUCE) has the form of a large, leaf-like cell surface (Fig. 5, p. 12). Although the greater part of the *Confervoideae* live in fresh or salt water, a few aerial forms (*Chroolepideae*) grow on stones, trunks of trees, and, in the tropics, on leaves. To this family belongs *Trentepohlia* (or *Chroolepus*) *Jolithus*, often found growing on stones in mountainous regions. The cell filaments of this species appear red on account of the hæmatochrome they contain, and possess a violet-like odour.

The asexual reproduction of the *Confervoideae* is accomplished by the formation of ciliated swarm-spores, although in many cases they may also develop resistant resting-spores.

Sexual reproduction is effected either by the fusion of planogametes or the sexual cells are differentiated as non-motile egg-cells and motile spermatozoids.

Ulothrix zonata (Fig. 246, *A*) and *Cladophora glomerata* (Fig. 247) are two of the commonest filamentous Algæ. The filaments of *Ulothrix* exhibit no pronounced apical growth; they are unbranched, attached by a rhizoid cell, and consist of single rows of short cells. Each cell contains a nucleus and one band-shaped, green chromatophore in the form of an almost complete hollow cylinder. The clumps of *Cladophora*, on the other hand, which may attain the length of a foot, consist of branched filaments with apical growth. Branches arise from the upper end of the elongated cells, which contain a number of nuclei (Fig. 61) and numerous polygonal chromatophores. Both species are isogamous.

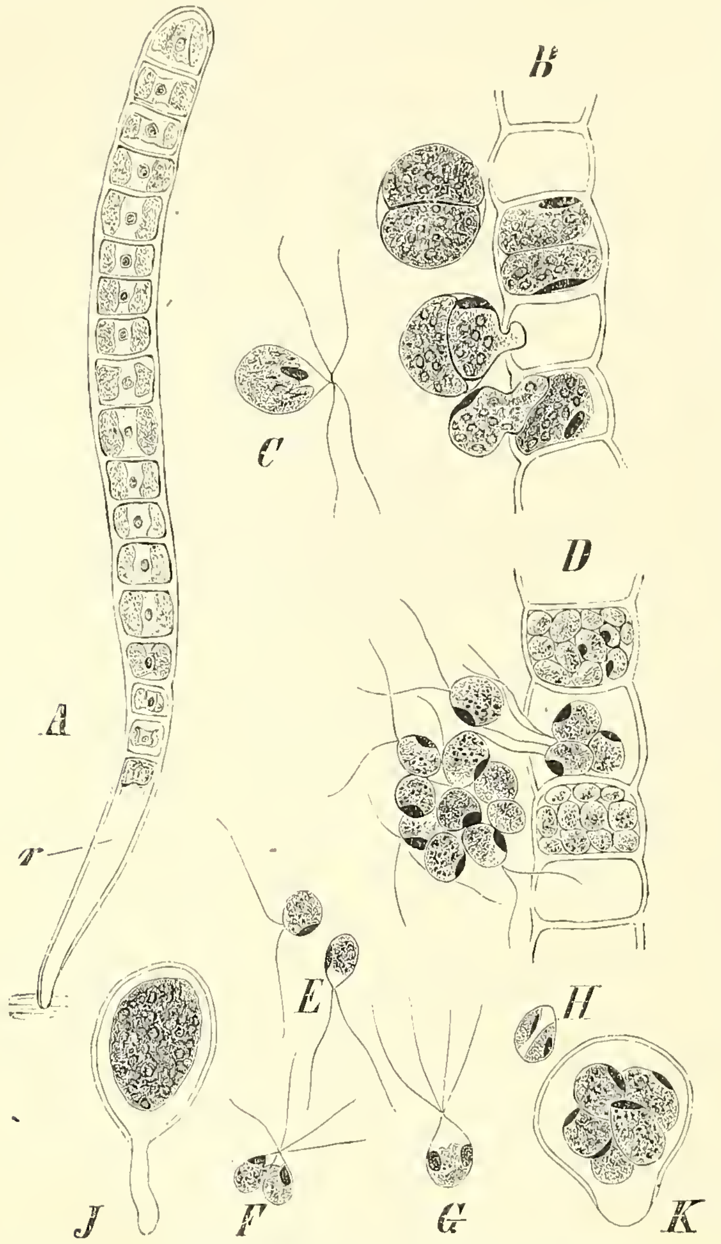


Fig. 246.—*Ulothrix zonata*. *A*, Young filament with rhizoid cell *r* (× 300); *B*, portion of filament with escaping swarm-spores; *C*, single swarm-spore; *D*, formation and escape of gametes; *E*, gametes; *F*, *G*, conjugation of two gametes; *H*, zygote; *J*, zygote after period of rest; *K*, zygote after division into swarm-spores. (After Dodel-Port, *B*-*K* × 482.)

In *Ulothrix zonata* (17, 18) (Fig. 246) asexual reproduction is effected by means of swarm-spores, which have four cilia (*C*), and are formed by division in any cell of the filament. A single cell produces 1-8 swarm-spores, and in the larger forms 16-32 swarm-spores may originate from each cell. The swarm-spores escape through a lateral opening (*B*) formed by absorption of the cell wall, and, after swarming, give rise to new filaments. The sexual swarm-cells, or planogametes, are formed in a similar manner by the division of the cells, but in much greater numbers. They are also smaller, and possess only two cilia (*E*). In other respects they resemble the swarm-spores, and possess a red eye-spot and one chromatophore. By the conjugation of the planogametes in pairs, zygotes (*F*-*H*) are produced, which, after drawing in their cilia, round themselves off and become invested with a cell wall. After a shorter or longer period of rest the zygotes are converted into unicellular germ plants (*J*), and give rise to several swarm-spores (*K*), which in turn grow out into new filaments. Under some conditions the planogametes can give rise to new plants parthenogenetically without conjugating. Further, the filaments can, in addition to the swarm-spores with four cilia described above, produce others of smaller size (microzoospores) which resemble the gametes. These possess four or two cilia, and as a rule die if the temperature of the medium is above 10° ; below this temperature they come to rest after a few days and proceed to germinate slowly. This Alga is thus of interest from the incomplete sexual differentiation exhibited by its gametes.

The genera *Oedogonium* (19) and *Bulbochaete* may be quoted as examples of oogamous *Confervoideae*. While the thallus of the latter is branched, the numerous species of *Oedogonium* consist of unbranched filaments, each cell of which possesses one nucleus and a single parietal chromatophore composed of numerous united bands. The asexual swarm-spores of *Oedogonium* are unusually large and have a circlet of cilia around their colourless anterior extremity (Fig. 248, *B*). In this case the swarm-spores are formed singly, from the whole contents of any single cell of the filament (*A*), and escape by the rupture of the cell wall. For the purpose of sexual reproduction, on the other hand, special cells become swollen and differentiated into barrel-shaped oogonia.

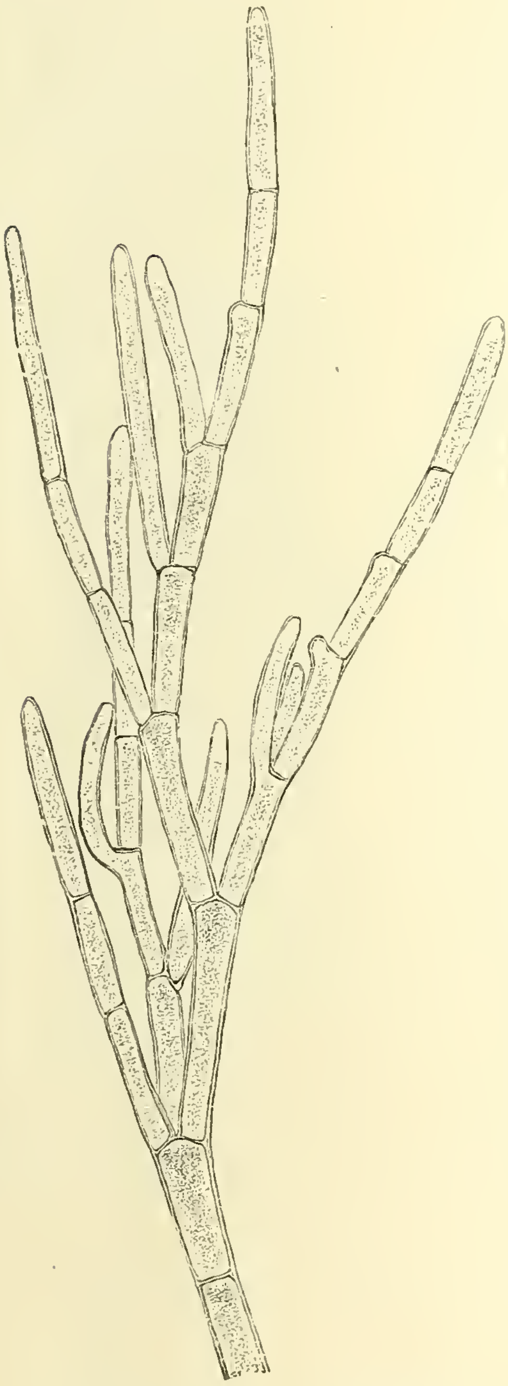


FIG. 247.—Portion of *Cladophora glomerata*. (× 48.)

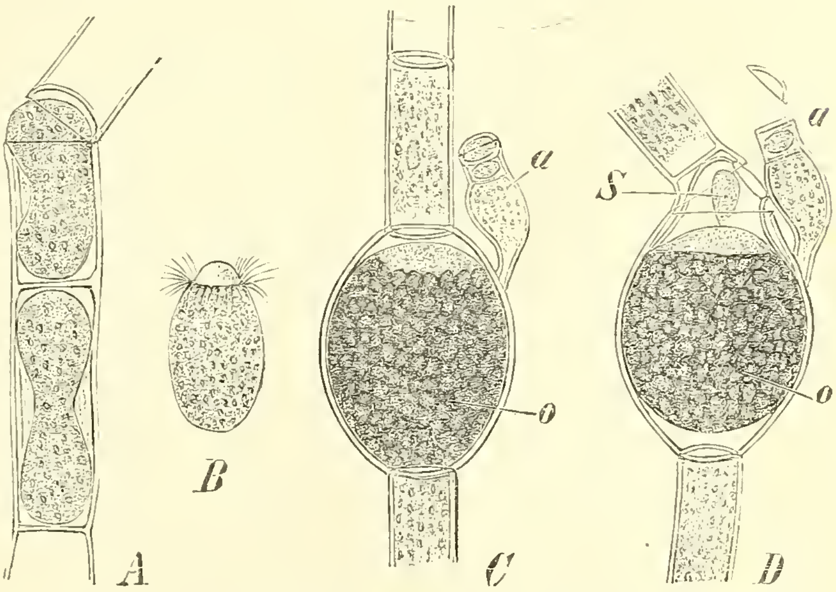


FIG. 248.—*A*, *B*, *Oedogonium*: *A*, escaping swarm-spores; *B*, free swarm-spore. *C*, *D*, *Oedogonium ciliatum*: *C*, before fertilisation; *D*, in process of fertilisation; *o*, oegonia; *a*, dwarf-males; *S*, spermatozoid. (After PRINGSHEIM, × 350.)

A single large egg-cell with a colourless receptive spot is formed in each oogonium by the contraction of its protoplasm, while the wall of the oogonium becomes perforated by an opening at a point opposite the receptive spot of the egg. At the same time, other, generally shorter, cells of the same or another filament become converted into antheridia. Each antheridium gives rise either to one or, as is more generally the case, to two spermatozoids. The spermatozoids are smaller than the asexual swarm-spores, but have a similar circlet of cilia. They penetrate the opening in the oogonium and fuse with the egg-cell, which then becomes transformed into a large, firm-walled oospore. On the germination of the oospore its contents become divided into four swarm-spores, each of which gives rise to a new cell filament. In the adjoining figure (Fig. 249) a germinating oospore of *Bulbochaete* with four swarm-spores is represented.

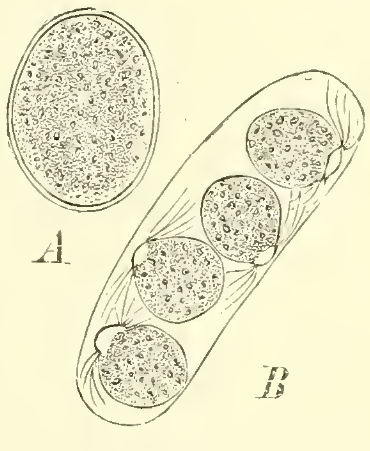


FIG. 249.—*Bulbochaete intermedia*. *A*, Oospore; *B*, formation of four swarm-spores in the germinating oospore. (After PRINGSHEIM, × 250.)

In some species of *Oedogonium* the process of sexual reproduction is more complicated, and the spermatozoids are produced in so-called DWARF MALES. These are short filaments (Fig. 248, *C*, *a*) consisting of but few cells, and are developed from asexual swarm-spores (ANDROSPORES) which, after swarming, attach themselves to the female filaments, or even to the oogonia. In the upper cells of the dwarf-male filaments thus derived from the androspores, spermatozoids are produced which are set free by the opening of a cap-like lid (Fig. 248, *D*, *a*).

In consequence of the greater complication in the process of their sexual reproduction, the oogamous *Confervoideae* are considered to represent a higher stage of development than the isogamous forms.

Order 3. Siphoneae

The *Siphoneae* are distinguished not only from the *Chlorophyceae* but from all other Algæ by the structure of their thallus, which, although more or less profusely branched, is usually composed of but one cell, or if it is multicellular, each cell contains several nuclei. In the first case, the cell wall encloses a single protoplasmic mass, in the peripheral portions of which are embedded the many nuclei and numerous small green chromatophores. In the class of the *Hyphomycetes*, the *Phycomycetes*, or Algal Fungi, exhibit the same characteristic structure, and may be regarded as possibly derived from the *Siphoneae.*

The *Siphoneae* comprise about forty genera, which, however, do not include a great number of species. They live for the most part in salt-water, although the species of *Vaucheria* thrive in fresh-water or are found as terrestrial Algæ, growing on damp soil. *Botrydium* is also terrestrial, while some forms of the *Siphoneae* are endophytic, and live in the leaves of the higher plants.

Sexual reproduction has advanced to oogamy only in the genus *Vaucheria;* in other instances it is isogamous and the conjugating gametes are alike in form and size.

The simplest form of the *Siphoneae* is represented by *Botrydium* ([18]), to which genus belongs the cosmopolitan species *Botrydium granulatum.* This Alga grows on damp clayey soil, where it forms groups of green, balloon-shaped vesicles about two millimetres in breadth. The vesicles are attached to the ground by prolongations from the base, in the form of a branching system of filamentous rhizoids devoid of chromatophores (Fig. 250, *A*). The cell walls of the vesicle and rhizoids of each individual enclose but one protoplast; this has numerous small nuclei, and in the upper part numerous chlorophyll granules which contain pyrenoids when young, but form no starch but a fatty oil. Multiplication may take place vegetatively, by budding, resulting in the outgrowth of a new vesicle from the aerial portion of the thallus. After enlarging considerably in size and sending down rhizoids into the substratum, the young plantlet isolates itself from the mother vesicle by a new cell wall. Asexual reproduction is provided for by the formation of swarm-spores. In this process the whole plant becomes converted into a single sporangium by the division of its protoplasmic contents into numerous swarm-spores, which make their escape through an opening at the apex.

Each swarm-spore has two to four chromatophores, but only a single cilium, which is situated at its anterior, colourless end (Fig. 250, *B*). The formation of swarm-spores occurs only when the thallus is covered with water. After coming to rest the heliotactic swarmers invest themselves with a cell wall and give rise to new plantlets. Whether sexual gametes are also formed is not at present certain.

Klebs has shown that another species, *Protosiphon botryoides*, usually occurs along with *Botrydium*. The rhizoid of this species is, as a rule, unbranched, and it contains a single reticulate chromatophore. *Protosiphon* produces planogametes, which unite in pairs to form resting zygotes of star-like shape (Fig. 250, *C*).

The thallus of *Vaucheria* (^{20}), the only oogamous genus of the *Siphoneae*, also consists of a single cell attached to the substratum by means of colourless rhizoids; but its aerial portion, unlike that of *Botrydium*, is branched and filamentous.

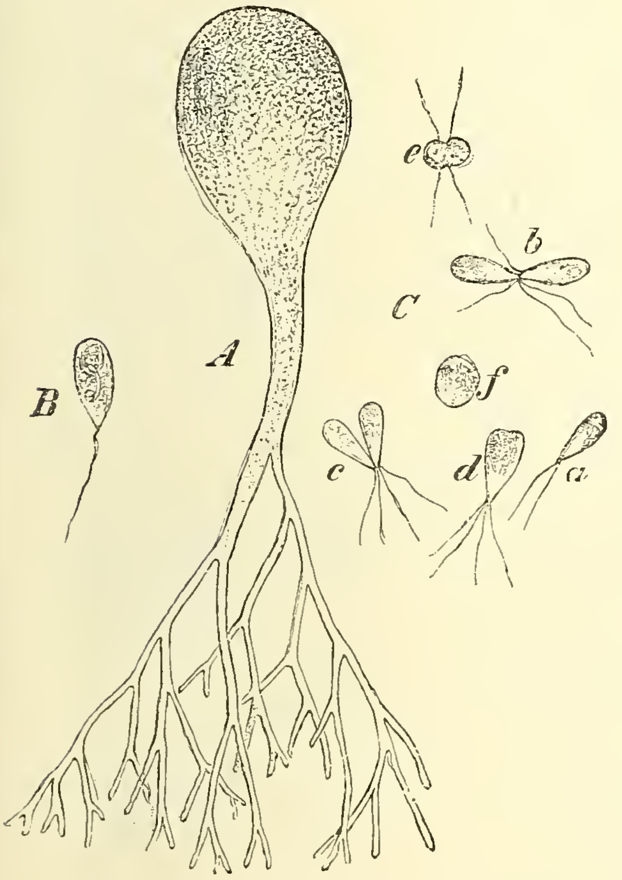


Fig. 250.—*A*, *B*, *Botrydium granulatum*. *A*, The whole plant; *B*, swarm-spore; *C*, *Protosiphon botryoides*, planogametes; *a*, a single gamete; *b-e*, two gametes in process of fusion; *f*, zygote. (*A* × 28; *B*, *C* × 540.)

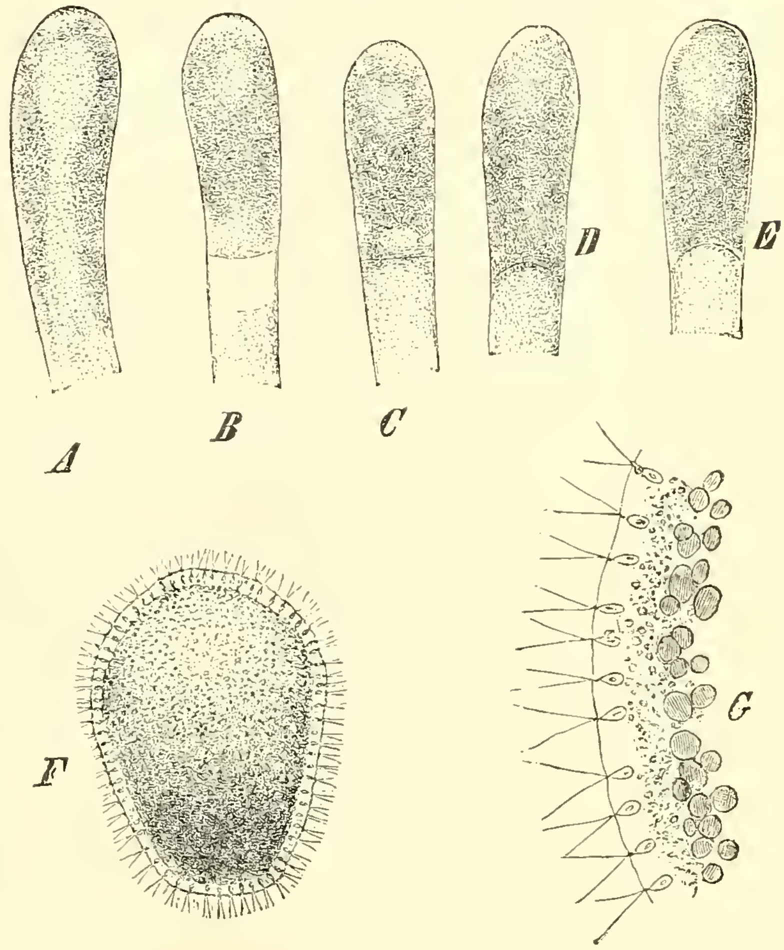


Fig. 251.—*Vaucheria sessilis*. *A*, *B*, A sporangium in process of formation; *C*, *D*, *E*, formation of a swarm-spore (× 95); *F*, swarm-spore (× 25); *G*, portion of the colourless peripheral protoplasm in the anterior end of the swarm-spore (× 950).

The swarm-spores of *Vaucheria* are developed in special sporangia, cut off from the swollen extremities of lateral branches by means of transverse walls (Fig. 251, *A-E*). The whole contents of such a sporangium become converted into a single green swarm-spore. The wall of the sporangium then ruptures at the apex, and the swarm-spore rotating on its longitudinal axis forces its way through the opening. The swarm-spore (*F*) is so large as to be visible to the naked eye, and contains numerous nuclei embedded in an investing layer of colourless protoplasm. It is entirely surrounded with a fringe of cilia, which protrude in pairs, one pair opposite each nucleus (*G*). Morphologically the swarm-spores of *Vaucheria* correspond to the collective individual spores of *Botrydium*.

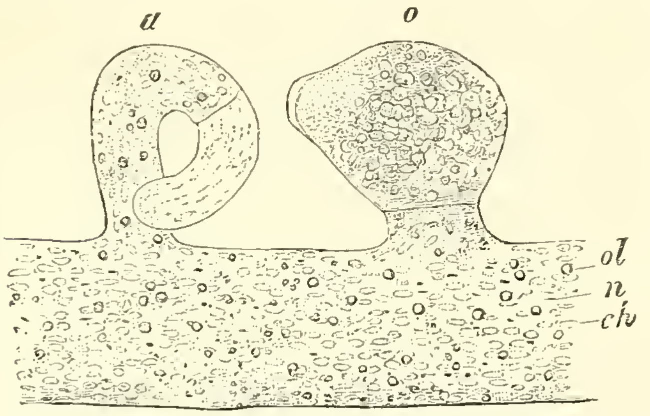


Fig. 252.—*Vaucheria sessilis.* Portion of a filament with an oogonium, *o*; antheridium, *a*; *ch*, chromatophores; *n*, cell nuclei; *ol*, oil globules. (× 240.)

The sexual reproduction of *Vaucheria* is not effected, like that of the other *Siphoneae*, by the conjugation of motile gametes, from which, however, as the earlier form of reproduction, it may be considered to have been derived. The oogonia and antheridia first appear as small protuberances, which grow out into short lateral branches and become separated by means of septa from the rest of the thallus (Fig. 252, *o*, *a*). At first, according to Oltmanns, the rudiment of an oogonium contains numerous nuclei, of which all but one, the nucleus of the future egg-cell, retreat again into the main filament before the formation of the separative septum. In its mature condition the oogonium has on one side a beak-like projection containing only colourless protoplasm, while the rest of the oogonium is filled with numerous chromatophores and oil globules. The apical portion of the projection becomes mucilaginous, and is finally ruptured by the extrusion of a colourless drop of protoplasm from the egg-cell which, in the meantime, has been formed by the contraction of the contents of the oogonium. The antheridia, which are also multinuclear, are more or less coiled (*a*), and open at

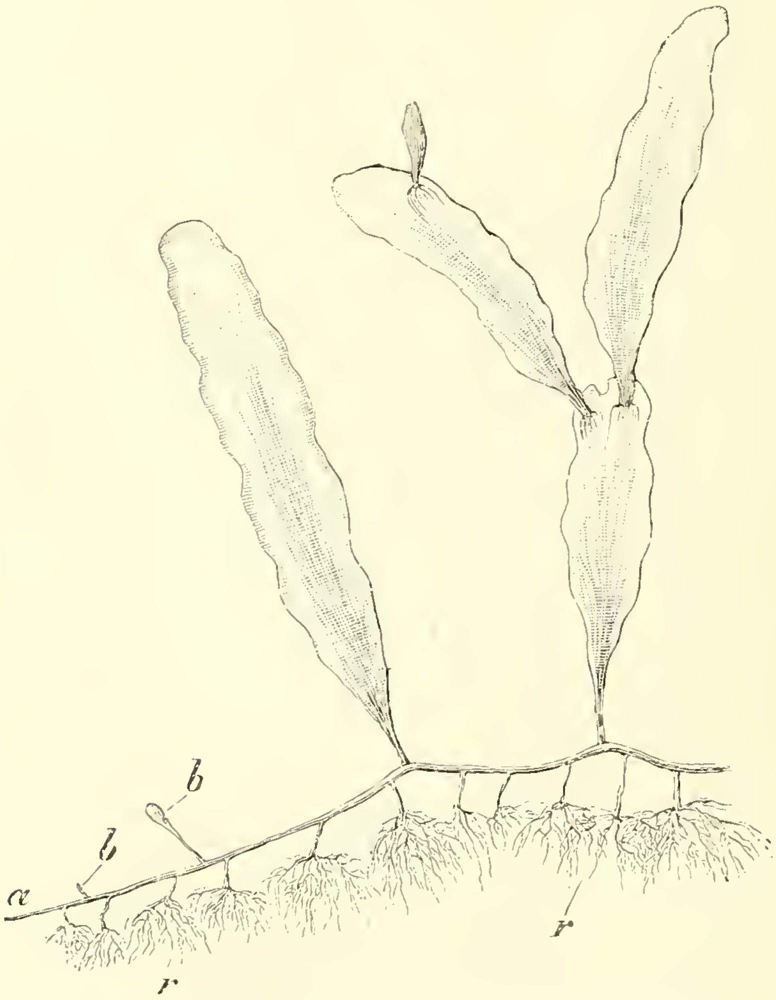


Fig. 253.—*Caulerpa prolifera.* The shaded lines on the thallus leaves indicate the currents of protoplasmic movement; *a*, growing apex of the thallus axis; *b*, *b*, young thallus lobes; *r*, rhizoids. (½ nat. size.)

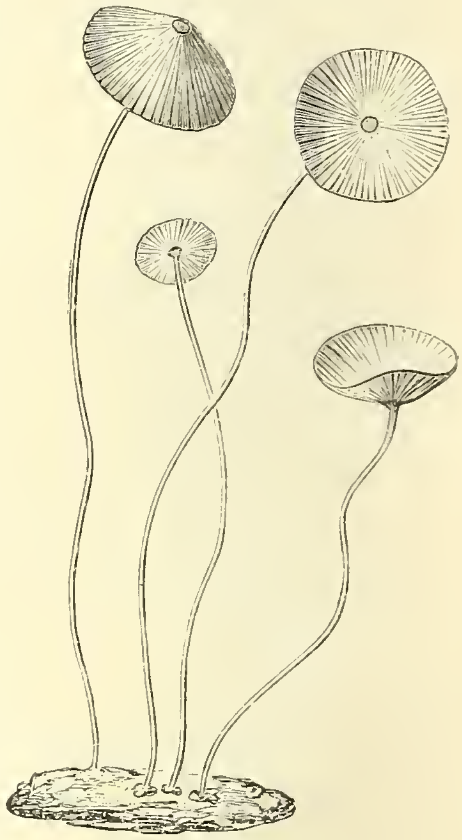


Fig. 254.
Acetabularia mediterranea.
(Nat. size.)

the tip to set free their slimy contents, which break up into a number of swarming spermatozoids. The spermatozoids, which are very small and entirely devoid of chromatophores, consist chiefly of nuclear substance. They collect around the receptive-spot of the egg-cell, into which one spermatozoid finally penetrates. After the egg-cell has been fertilised by the fusion of its nucleus with that of the spermatozoid, it becomes invested with a wall and converted into a resting oospore.

The marine *Siphoneae*, on account of the more complicated segmentation of their thallus, afford one of the most interesting types of algal development. The genus *Caulerpa* (21), represented by many species inhabiting the warmer water of the ocean, has a thick, creeping main axis or stem. Increasing in length by apical growth, the stem-like portion of the thallus gives off from its under surface profusely branched colourless rhizoids, while, from its upper side, it produces green thalloid segments which vary in shape in the different species. In *Caulerpa prolifera* (Fig. 253) these outgrowths are leaf-like, are frequently proliferous, and have only a limited growth. In other species they are pinnately lobed or branched. The whole thallus, however branched and segmented it may be, encloses but one cell-cavity, which is, however, often traversed by a network of cross-supports or trabeculæ.

The genus *Bryopsis*, on the other hand, has a delicate, pinnately-branched thallus. Although originally unicellular, the thallus develops lateral tubular branches that eventually become septated from it by the formation of transverse walls.

Other marine *Siphoneae* become encrusted with calcium oxalate and calcium carbonate, and bear a resemblance to coral, *e.g. Halimeda Opuntia*, which resembles *Opuntia* on a small scale. *Acetabularia mediterranea* (22), also one of the calcareous *Siphoneae*, has a stalked umbrella-like thallus (Fig. 254) attached firmly to the substratum by means of rhizoids. The disc consists of a number of closely-crowded tubular outgrowths radiating from the tip of the stalks, in which are developed the non-motile spores, the so-called aplanospores. These are liberated when the disc falls to pieces, and form gametangia, and in the latter planogametes, which conjugate in pairs, are developed.

CLASS IX

Phaeophyceae (Brown Algæ) (13, 23)

With the exception of a very few fresh-water species, the *Phaeophyceae* are only found in salt-water. They are all fixed, and attain their highest development in the colder waters of the ocean. They show great diversity in the form and structure of their vegetative body. The simplest representatives of this class (*e.g.* the genus *Ectocarpus*) closely resemble the *Confervoideae*, in having a filamentous thallus consisting of a branched or unbranched row of simple cells. Some *Phaeophyceae*, again, have a cylindrical, copiously branched, multicellular thallus (*e.g. Cladostephus*, whose main axes are thickly beset with short multicellular branches, Fig. 7); while in other cases the multicellular thallus is band-shaped and dichotomously branched (*e.g. Dictyota*,

Fig. 8). Growth in length in both of these forms ensues from the division of a large apical cell (Figs. 7 and 161). Other species, again, are characterised by disc-shaped or globose thalli.

The *Laminariaceae* and *Fucaceae* include the most highly-developed forms of the *Phaeophyceae.* To the first family belongs the genus *Laminaria* found in the oceans of northern latitudes. The large-stalked thallus of the Laminarias resembles an immense leaf; it is attached to the substratum by means of branched, root-like hold-fasts, developed from the base of the stalk.

Fig. 255.—*Laminaria digitata*, forma *Cloustoni*, North Sea. (Reduced $\frac{1}{3}$. OFFICINAL.)

In the case of *Laminaria digitata* (Fig. 255), and similarly in other species, a zone at the base of the palmately divided leaf-like expansion of the thallus retains its meristematic character, and by its intercalary growth produces a succession of new laminæ. Each older lamina becomes pushed up and gradually dies, while a new one takes its place and becomes in turn palmately divided by longitudinal slits. The large size of their thalli is also characteristic of the Laminarias: *L. saccharina* (North Sea), for instance, is frequently 3 m. long and the stalk more than 1 cm. thick.

The greatest dimensions attained by any of the *Phaeophyceae* are exhibited by certain of the Antarctic *Laminariaceae.* Of these, *Macrocystis pyrifera* (Fig. 256) is noted for its gigantic size; rising obliquely upwards to the surface of the water from the sloping sides of elevations in the ocean bed; its floating thallus has a length of 200 to 300 m. With the exception of a naked lower portion this bears numerous long pendent lobes, each of which is provided at the base with a large bladder-like float filled with air. Even more remarkable, on account of their tree-like character, are the Antarctic species of *Lessonia*, in which the main axis is as thick as a man's arm; from it are given off lateral branches with hanging leaf-like segments. The plant attains a height of several metres, and has a tree-like habit of growth.

The *Fucaceae*, although relatively large, do not compare with the *Laminariaceae* in size. As examples of well-known forms of this order may be cited *Fucus vesiculosus* (Fig. 260, *b*), which has a band-shaped, dichotomously branching thallus with air-bladders, and *Fucus platycarpus* without bladders. Both species are fastened to the substratum by discoid hold-fasts, and growing sometimes over 1 metre long, are found covering extended areas of the littoral region of the sea-coast. *Sargassum*, a related genus chiefly inhabiting tropical oceans, surpasses the other brown sea-weeds, and even all other Algæ, in the segmentation of its thallus, and in this respect it bears a close resemblance to the higher plants. The thallus of *Sargassum* shows in fact a distinction into slender branched cylindrical axes with lateral outgrowths, which, according to their function, are differentiated as foliage, bracteal, or fertile segments, or as air-bladders. Various species of *Sargassum* which have been swept away from the coast by currents, finally collect in large floating masses in quiet regions of the ocean (Sargasso Sea). *Sargassum bacciferum* is carried even to the coast of Europe.

The cells of the *Phaeophyceae* have usually but one nucleus. They are supplied with a larger or smaller number of chromatophores, which, in addition to chlorophyll, contain a brown pigment, PHYCOPHAEIN, which imparts to the Algæ a yellowish-brown or dark brown colour. Numerous grains of a semifluid substance, to which the name FUCOSAN has been given, appear as the product of assimilation. This substance appears to be a carbohydrate, and, according to HANSTEEN (²⁴), originates in the chromatophores. Among the more highly-developed forms the thallus exhibits a fairly highly differentiated anatomical structure. The outer cell layers, as a rule, function as an assimilatory tissue, the inner cells as storage reservoirs. In some species the axial cells of the thallus are arranged in definite strands with sieve-tube like elements and true sieve-tubes (²⁵).

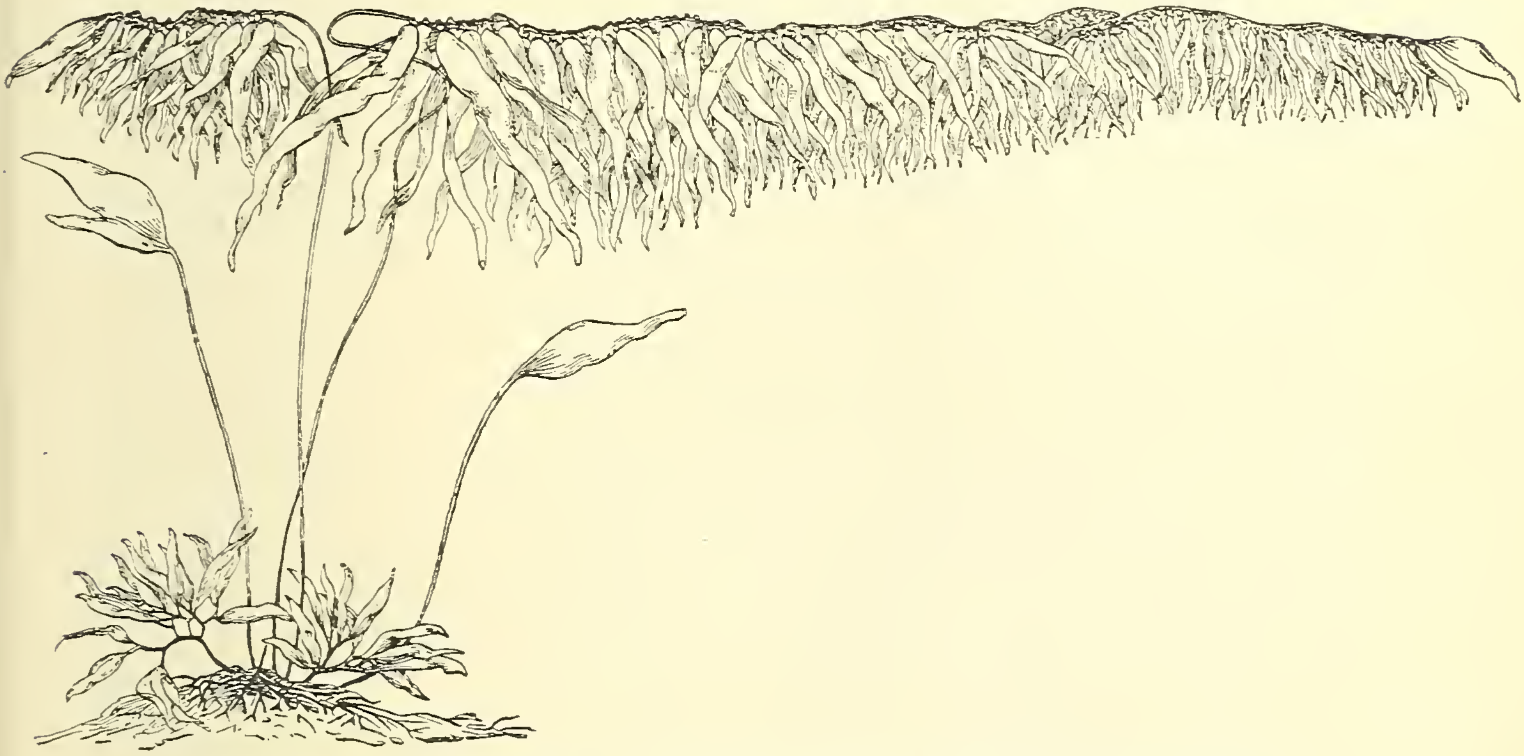


FIG. 256.—*Macrocystis pyrifera*, Ag. (Greatly reduced. After HOOKER and HARVEY.)

According to the manner of their sexual and asexual reproduction, the *Phaeophyceae* fall naturally into three orders.

Order 1. Phaeosporeae (²⁶)

In this order are included the Laminarias, as well as the majority of the other *Phaeophyceae*. Asexual multiplication is effected by means of swarm-spores, which are produced in large numbers in simple, so-called unilocular sporangia ; they have a red eye-spot, a chromatophore, and two LATERALLY INSERTED cilia (Fig. 257).

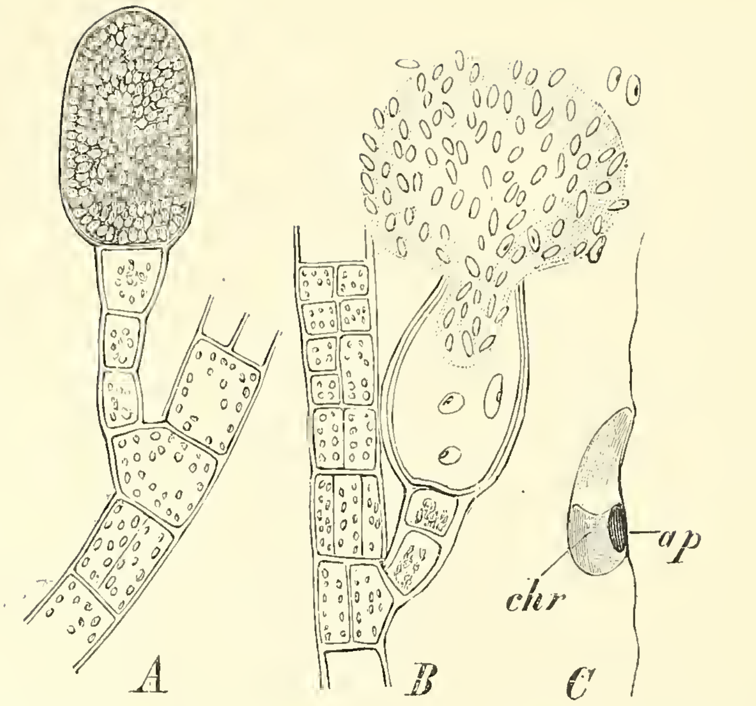


FIG. 257.—*Cladostephus verticillatus.* *A*, Closed sporangium (× 280); *B*, swarm-spores escaping from a sporangium (× 280); *C*, a single swarm-spore (× circa 2000), with red eye-spot *ap*, and yellow chromatophore *chr*. (After PRINGSHEIM.)

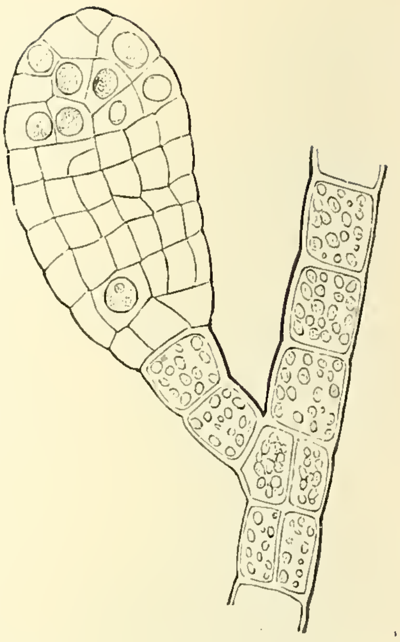


FIG. 258.—*Cladostephus verticillatus*, with gametangium partly discharged. (After PRINGSHEIM, × 500.)

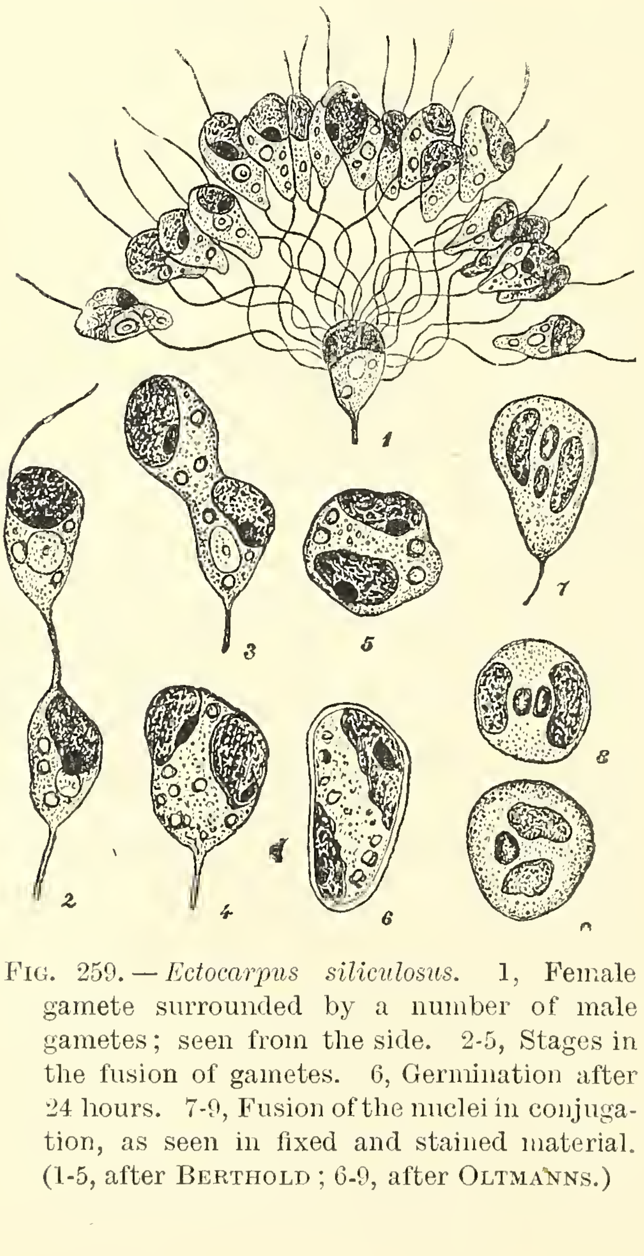


FIG. 259.—*Ectocarpus siliculosus.* 1, Female gamete surrounded by a number of male gametes; seen from the side. 2-5, Stages in the fusion of gametes. 6, Germination after 24 hours. 7-9, Fusion of the nuclei in conjugation, as seen in fixed and stained material. (1-5, after BERTHOLD; 6-9, after OLTMANNS.)

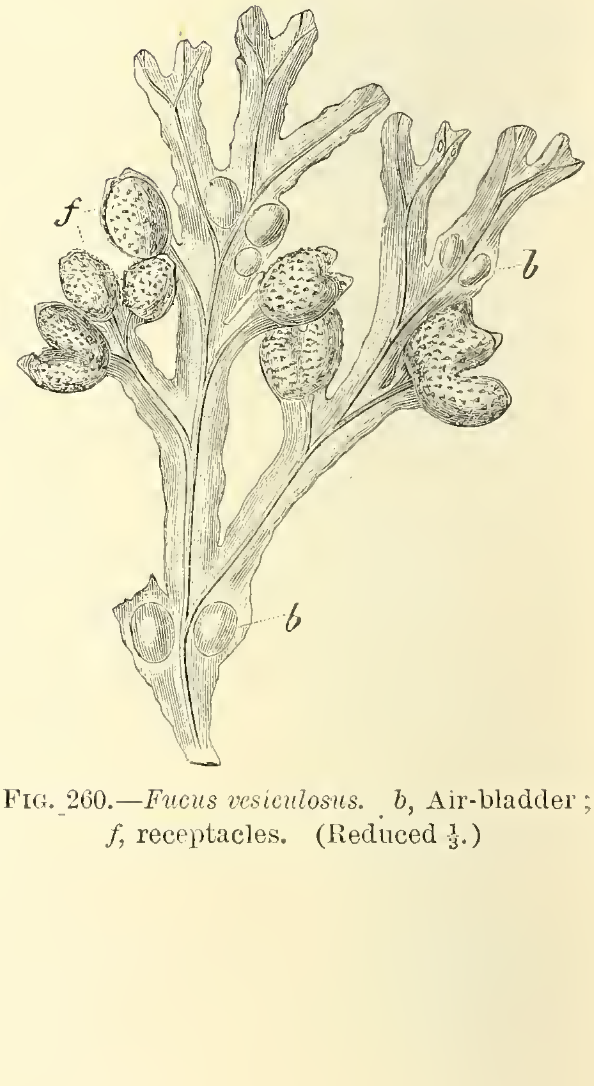


FIG. 260.—*Fucus vesiculosus.* *b*, Air-bladder; *f*, receptacles. (Reduced $\frac{1}{3}$.)

In addition to unilocular sporangia, multilocular sporangia are produced in the *Phaeosporeae* (Fig. 258). Each cell of the latter produces a single swarm-spore, rarely several. The conjugation of these swarm-spores has been observed in some genera. On this account these swarm-spores must be termed gametes, and the corresponding sporangia gametangia. The degree of sexual differentiation varies, and in some cases the gametes can germinate without conjugating, as was seen to occur in *Ulothrix* among the *Chlorophyceae.*

Ectocarpus siliculosus (Fig. 259) will serve as an example of the mode of conjugation of gametes produced from multilocular gametangia. The gametes are similar in form, but their different behaviour allows of their destinction into male and female. The female gamete becomes attached to a substratum, and numerous male gametes gather around it (Fig. 259, 1). Ultimately a male gamete fuses with the female to form a zygote (Fig. 259, 2-9). This contains after the fusion a single nucleus, but two chromatophores, and soon becomes attached and surrounded by a cell wall; it grows into a new plant.

In other *Phaeophyceae* the distinction between the two kinds of gametes is expressed in their shape and size. The *Cutleriaceae* afford a particularly good transition from isogamy to oogamy (^{27}).

Order 2. Fucaceae (^{28})

Asexual reproduction is wanting in this order, while sexual reproduction is distinctly oogamous. The oogonia and antheridia, as in *Fucus vesiculosus* and *platycarpus*, for example, are formed in special flask-shaped depressions termed CONCEPTACLES, which are crowded together below the surface in the swollen tips or RECEPTACLES of the dichotomously branched thallus (Fig. 260, *f*). The conceptacles of *F. platycarpus* (Fig. 261) contain both oogonia and antheridia, while *F. vesiculosus*, on the contrary, is diœcious. From the inner wall of the conceptacles, between the oogonia and antheridia, spring numerous, unbranched, sterile hairs or PARAPHYSES, of which some protrude in tufts from the mouth of the conceptacle (Fig. 261, *p*). The antheridia are oval in shape, and are formed in clusters on special short and much-branched filaments (Figs. 261, *a*, 262, *C*). The contents of each antheridium separate into a large number of spermatozoids, which are discharged in a mass, still enclosed within the inner layer of the antheridial wall (Fig. 262, *B*). Eventually set free from this outer covering, the spermatozoids appear as somewhat elongated, ovate bodies, having two lateral cilia of unequal length and a red eye-spot

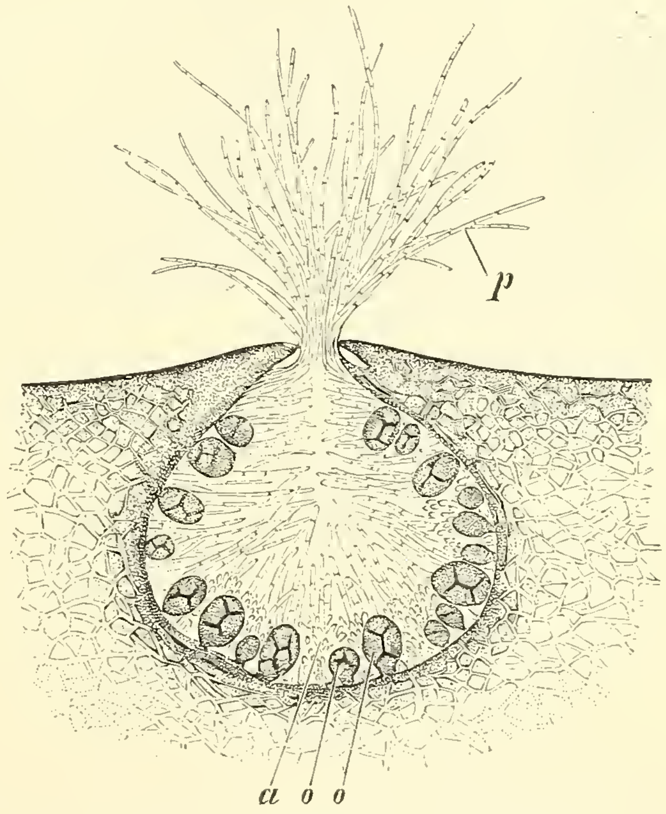


FIG. 261.—*Fucus platycarpus.* Monœcious conceptacle with oogonia of different ages (*o*), and clusters of antheridia (*a*); *p*, paraphyses. (After THURET, × circa 25.)

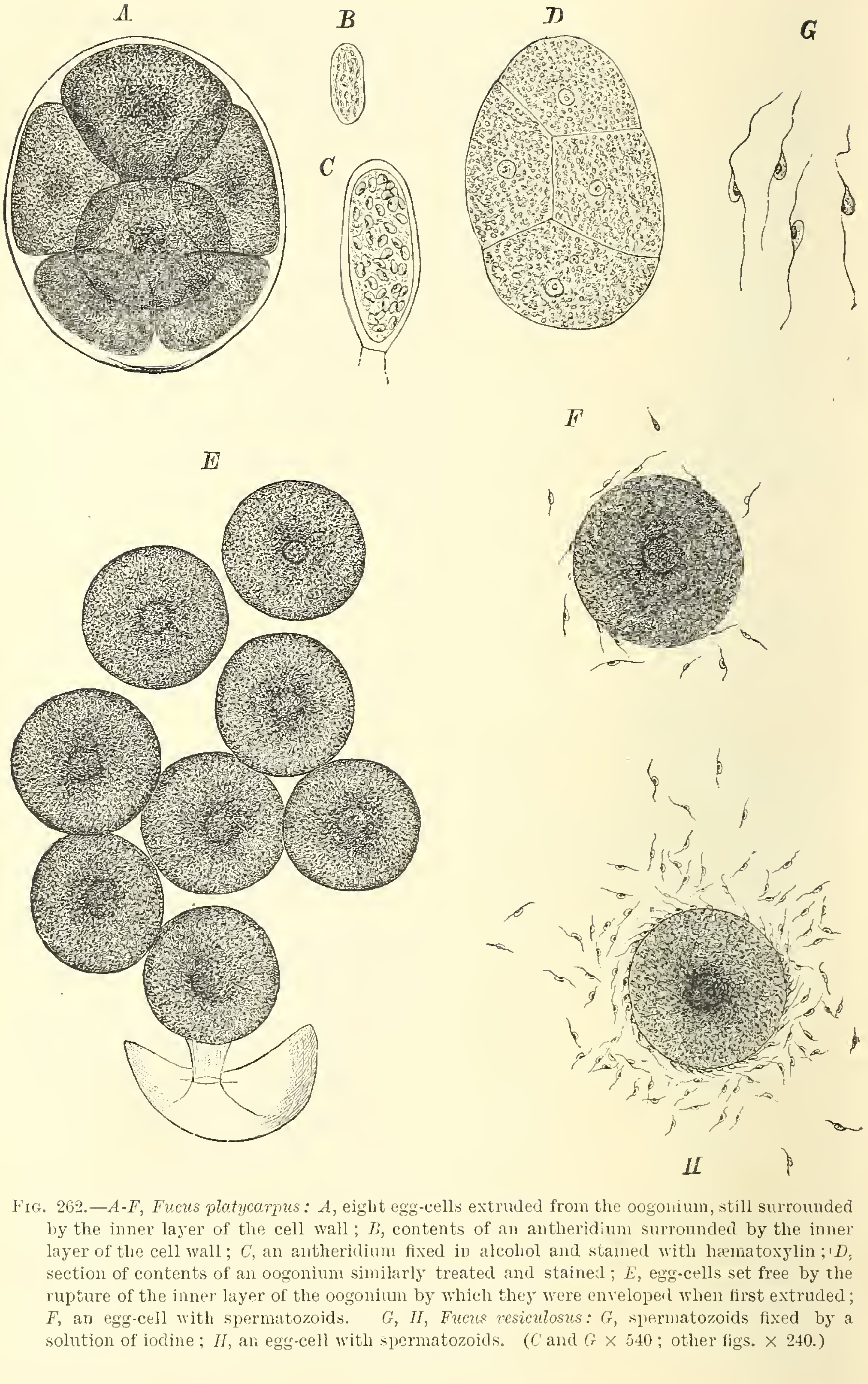


FIG. 262.—*A-F*, *Fucus platycarpus: A*, eight egg-cells extruded from the oogonium, still surrounded by the inner layer of the cell wall; *B*, contents of an antheridium surrounded by the inner layer of the cell wall; *C*, an antheridium fixed in alcohol and stained with hæmatoxylin; *D*, section of contents of an oogonium similarly treated and stained; *E*, egg-cells set free by the rupture of the inner layer of the oogonium by which they were enveloped when first extruded; *F*, an egg-cell with spermatozoids. *G*, *H*, *Fucus vesiculosus: G*, spermatozoids fixed by a solution of iodine; *H*, an egg-cell with spermatozoids. (*C* and *G* × 540; other figs. × 240.)

(*G*). The oogonia (Fig. 261, *o*) are nearly spherical, and are borne on a short stalk consisting of a single cell. They are of a yellowish-brown colour, and enclose eight spherical egg-cells which are formed by the division of the oogonium mother cell. The eggs are enclosed within a thin membrane when ejected from the oogonium (Fig. 262, *A*). This membranous envelope deliquesces at one end and, turning partly inside out, set free the eggs (Fig. 262, *E*). The spermatozoids then gather round the eggs in such numbers that by the energy of their movements they often set them in rotation (*F*, *H*). After an egg has been fertilised by the entrance of one of the spermatozoids it becomes invested with a cell wall, attaches itself to the substratum, and gives rise by division to a new plant. In the case of other *Fucaceae* which produce four, two, or even only one egg in their oogonia, the nucleus of each oogonium, according to OLTMANNS, nevertheless first divides into eight daughter nuclei, of which, however, only the proper number give rise to eggs capable of undergoing fertilisation.

Order 3. Dictyotaceae

In this order there are only a few forms (*e.g. Dictyota dichotoma*, Fig. 8). The asexual spores, of which only two or four are formed in a sporangium, are non-motile. The sexual organs are differentiated into oogonia and antheridia. Each oogonium contains a single egg-cell, which it eventually ejects. The multicellular antheridia produce a single spermatozoid from each cell; according to WILLIAMS (29) this differs from those of the other Brown Sea-weeds in possessing only one long cilium. The process of fertilisation has not as yet been observed.

Economic Uses.—The dried stalks of the officinal *Laminaria digitata*, forma *Cloustoni* (Pharm. germ.), are used as dilating agents in surgery. IODINE is obtained from the ash (varec, kelp) of various *Laminariaceae* and *Fucaceae*, and formerly soda. Many Laminarias are rich in MANNITE (*e.g. Laminaria saccharina*), and are used in its production, and also as an article of food by the Chinese and Japanese.

CLASS X

Rhodophyceae (Red Algæ) (13, 30)

The *Rhodophyceae* or *Florideae* constitute, like the *Phaeophyceae*, an independent group of Thallophytes, for whose phylogenetic derivation from the lower Algæ there is, as yet, no positive evidence. They are attached to some support, and almost exclusively marine, and specially characterise the lowest algal region on the coasts of all oceans, especially in temperate and tropical latitudes. A few genera (*e.g. Batrachospermum*, *Lemanea*, *Hildebrandtia*) grow in fresh-water streams.

The thallus of the Red Algæ exhibits a great variety of forms. The simplest forms are represented by branched filaments consisting of single rows of cells (*e.g. Callithamnion*). In other cases the branched filamentous thallus appears multicellular in cross-sections. In many other forms the thallus is flattened and ribbon-like (*e.g. Chondrus crispus*, Fig. 263 ; *Gigartina mammillosa*, Fig. 264) ; while in still other species it consists of expanded cell surfaces attached to a substratum.

FIG. 263.—*Chondrus crispus*. *s*, Oval cystocarps. (½ nat. size. *OFFICINAL*.)

The forms with more advanced segmentation resemble the vascular plants externally, and exhibit a differentiation into a cylindrical axis and flattened leaf-like thalloid branches which, as in *Delesseria* (*Hydrolapathum*) *sanguinea*, may even be provided with middle and lateral ribs (Fig. 9). In the autumn the wing-like expansions of the thallus are lost, but the main ribs persist and give rise to new branches in the succeeding spring. All the *Florideae* are attached at the base by means of rhizoidal filaments or discoid hold-fasts. The thalli of the *Corallinaceae*, which have the form of branched filaments or of flattened or tuberculate incrustations, are especially characterised by their coral-like appearance, owing to the large amount of calcium carbonate deposited in their cell walls. The calcareous *Florideae* are chiefly found on coasts exposed to a strong surf, especially in the tropics.

FIG. 264.—*Gigartina mammillosa*. *s*, Wart-shaped cystocarps. (¾ nat. size. *OFFICINAL*.)

The *Rhodophyceae* are usually red or violet ; sometimes, however, they have a dark purple or reddish-brown colour. Their chromatophores, which are flat, discoid, oval, or irregular-shaped bodies and closely crowded together in large numbers in the cells, contain a red pigment, PHYCOERYTHRIN, which completely masks the chlorophyll. True starch is never formed as a product of assimilation, its place being taken by other substances, very frequently, for example, by Floridean starch, in the form of spherical stratified grains which stain red with iodine. Oil-drops also occur. The cells may contain one or several nuclei.

Reproduction is effected either asexually by means of spores, or sexually by the fertilisation of female organs by male cells.

The asexual SPORES are non-motile ; they have no cilia and are simply naked, spherical cells. They are produced, usually, in groups of four, by the division of a mother cell or sporangium, from which they are in time set free by the transverse rupture of its walls. The sporangia themselves are nearly spherical or oval bodies seated on the thalloid filaments or embedded in the thallus. In consequence of their usual formation in fours, the spores of the *Florideae* are termed TETRASPORES (Fig. 265). They are analogous to the swarm-spores of other Algæ ; similar spores are found also in the *Dictyotaceae* among the brown Algæ.

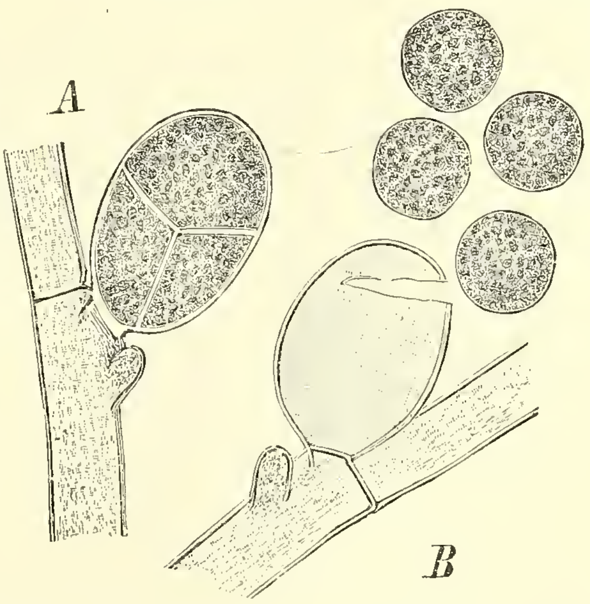


FIG. 265.—*Callithamnion corymbosum.* *A*, Closed sporangium ; *B*, empty sporangium with four extruded tetraspores. (After THURET.)

In the development of the sexual organs, particularly the female, the *Rhodophyceae* differ widely from the other Algæ. *Batrachospermum moniliforme*, a fresh-water form, may serve as an example to illustrate the mode of their formation. This Alga possesses a brownish thallus, enveloped in mucilage, and consisting of verticillately branched filaments. The sexual organs appear in the autumn and form on the branching whorls glomeruli or spherical bodies composed of short, radiating branches.

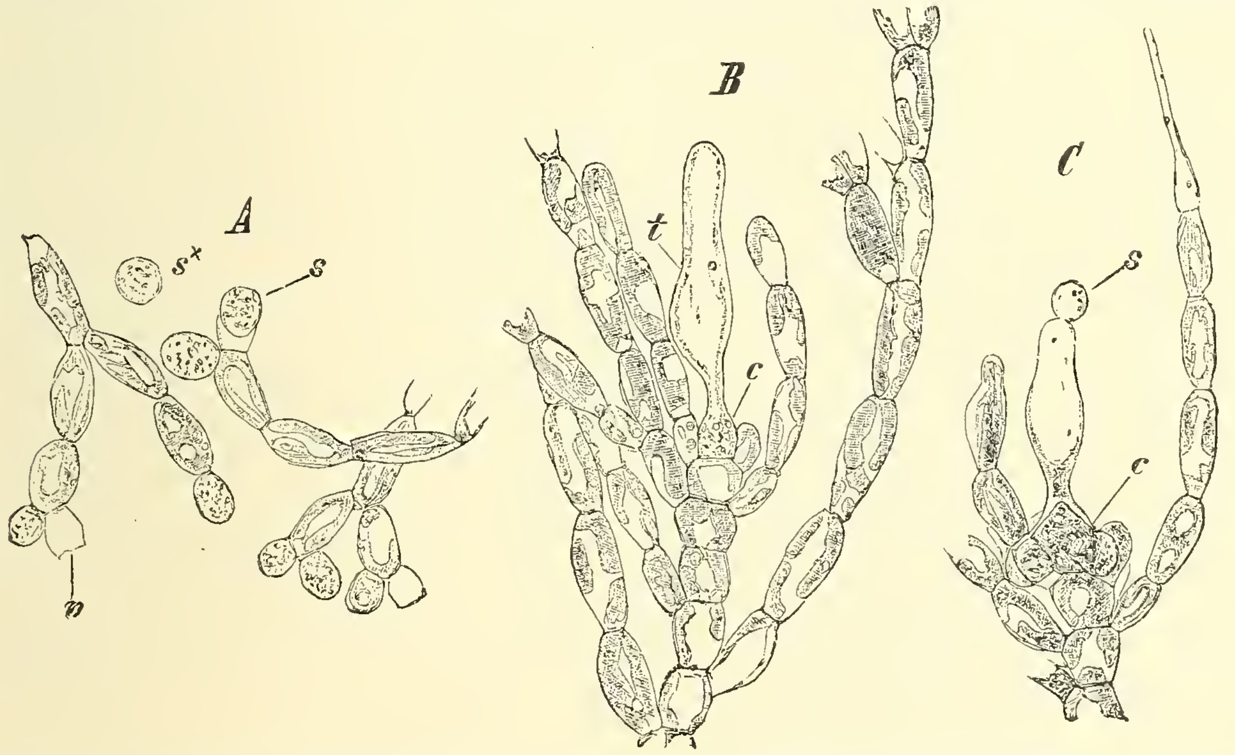


FIG. 266.—*Batrachospermum moniliforme.* *A*, Male branch with antheridia, isolated by pressure ; *s**, a spermatium ; *s*, a spermatium escaping from an antheridium ; *v*, an empty antheridium. *B*, female branch with an unfertilised carpogonium ; *c*, basal portion ; *t*, trichogyne of carpogonium. *C*, female branch with fertilised carpogonium ; *s*, the spermatium after the fusion of its contents with the trichogyne ; *c*, fertile filaments developing from the basal portion of the carpogonium. (× 540.)

The antheridia, also known as spermatangia (Fig. 266, *A*), are produced, usually in pairs, at the ends of the radiating branches of a glomerulus. Each antheridium consists of a single thin-walled cell, in which the whole of the protoplasm, as is the rule in all *Rhodophyceae*, is consumed in the formation of one uninuclear SPERMATIUM. The spermatia are nearly spherical, and immediately after their discharge from the antheridia (*A*, *v*, *s*) are naked, but afterwards become invested with a thin outer membrane or cell wall. They contain a single nucleus, and are non-motile, unlike the ciliated spermatozoids of the other Algæ, and have therefore received a distinctive name. In consequence of their incapacity for independent movement, they must be carried passively by the water to the female organs, which are situated near the antheridia at the ends of other branches. The female organ is called a CARPOGONIUM (Fig. 266, *B*), and consists of an elongated cell with a basal, flask-shaped portion (*c*) prolonged into a filament, termed the TRICHOGYNE (*t*). The basal portion contains the egg, which is provided with a large nucleus and chromatophores, while the trichogyne functions as a receptive organ for the spermatia, one or two of which fuse with it, and the contents, escaping through the spermatium wall, pass into the carpogonium. The sperm nucleus passes down the trichogyne and fuses with the nucleus of the egg-cell. The fertilised egg does not become converted directly into an oospore, but, as a result of fertilisation, numerous branching sporogenous filaments (gonimoblasts) grow out from the sides of the ventral portion of the carpogonium. At the same time, by the development of outgrowths from cells at the base of the carpogonium an envelope is formed about the fertile gonimoblasts. The whole product of fertilisation, including the surrounding envelope, constitutes the fructification, and is termed a CYSTOCARP. The profusely-branched gonimoblasts become swollen at the tips and give rise to spherical, uninuclear spores known as CARPOSPORES, which are eventually set free from the envelope. In the case of *Batrachospermum* the carpospores produce a filamentous protonema, the terminal cells of which give rise to asexual unicellular spores. These spores serve only for the multiplication of the protonema. Ultimately, however, one of the lateral branches of the protonema develops into the sexually differentiated filamentous thallus. The production of spores by the protonema is analogous to the formation of tetraspores by other *Florideae*.

The formation of the cystocarps and carpospores is much more complicated in the case of other genera, but in all cases, according to OLTMANNS, the carpospores are descended from the fertilised egg-cell. There are thus two generations distinguishable in the life-history of the *Florideae*, the sexual (gametophyte), which bears the egg-cells and the spermatia, and the asexual generation (sporophyte), derived from the fertilised egg-cell; the latter generation, which produces the carpospores, remains in connection with the parent plant. This type of alternation of generations is comparable with that found in Mosses and Ferns. The production of tetraspores is an asexual mode of reproduction of the sexual generation and precedes the formation of sexual organs.

Dudresnaya coccinea, which is found on the warmer coasts of Europe, has a branched, cylindrical thallus and will serve as an example of the more complicated mode of origin of the spore-bearing generation (Fig. 267). The carpogonial branches consist of about seven cells, the terminal one bearing a very long trichogyne. After fertilisation the carpogonial cell grows out into a filament, which elongates and becomes branched. This filament fuses with a number of special cells, characterised by their abundant contents, the AUXILIARY CELLS. The first of these lie in the carpogonial branch itself, the others in adjoining lateral branches. All the nuclei of the sporogenous filament are derived by division from that of the fertilised egg-cell. The successive fusions with auxiliary cells do not

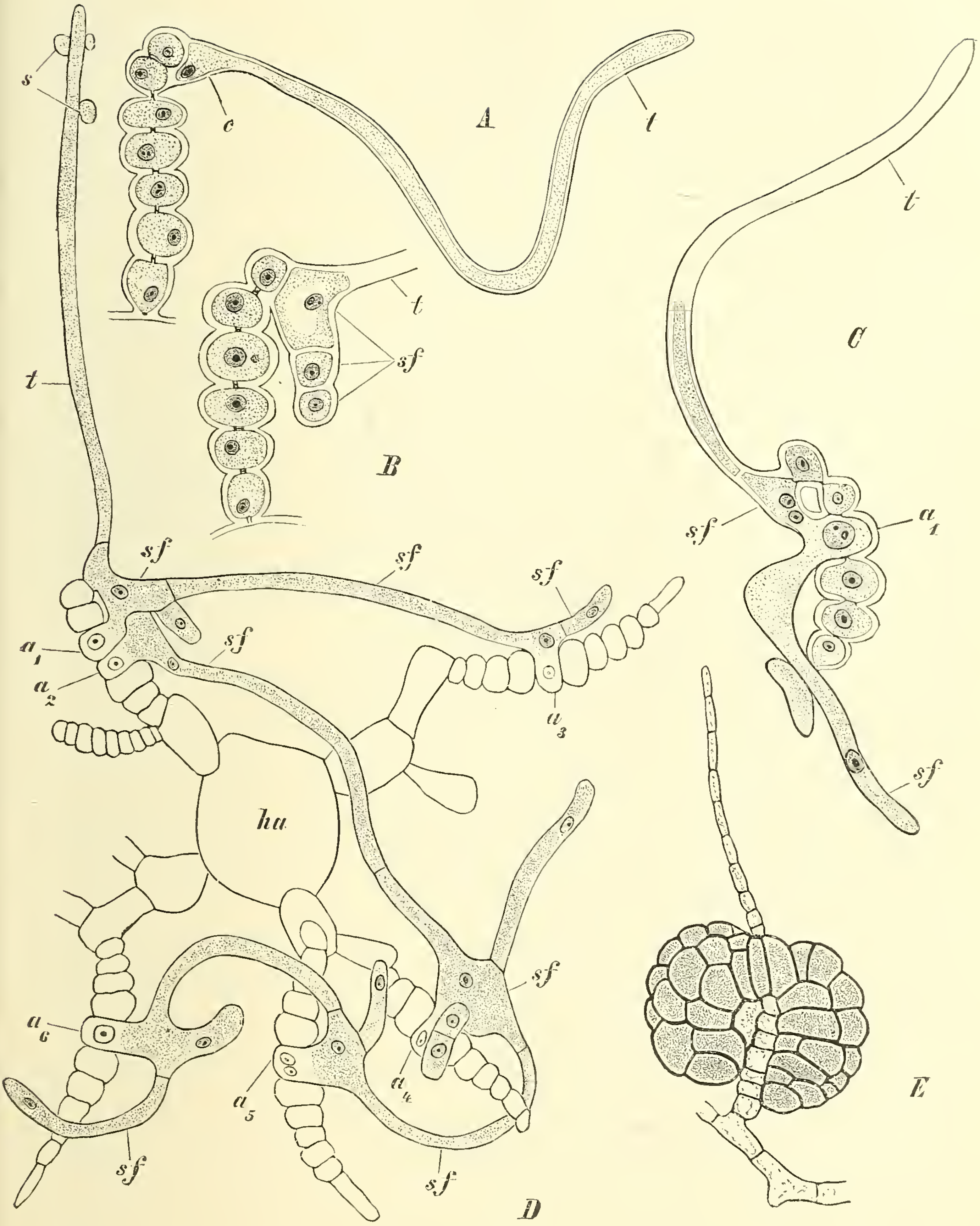


FIG. 267.—*Dudresnaya coccinea.* *A*, Carpogonial branch; *c*, carpogonium; *t*, trichogyne; *B*, carpogonium after fertilisation, grown out into the sporogenous filament (*sf*); *C*, fusion of the sporogenous filament with the first auxiliary cell (a_1); *D*, branching of the filament and fusion with six auxiliary cells (a_1-a_6); the cells a_3-a_6 are borne on branches originating from the axis *ha*. Diagrammatic. *E*, Ripe cluster of carpospores originating from one branch. (*A-D*, after OLTMANNS; *E*, after BORNET. *A-C*, × about 500; *D*, × 250; *E*, × 300.)

involve nuclear fusions but simply serve to nourish the sporogenous filament. A second and a third sporogenous filament may arise from the carpogonial cell. Two outgrowths now arise from each of the swollen cells of the sporogenous filament which fused with auxiliary cells. By further division of these outgrowths the spherical masses of carpospores, which subsequently become free, are derived (Fig. 267, *E*).

Harveyella mirabilis (31), a North Sea Floridean species, is of special interest. It grows as a parasite on another red seaweed, *Rhodomela subfusca*, on which it appears in the form of a small white cushion-like growth. As a result of its parasitic mode of life the formation of chromatophores has been entirely suppressed, and thus this plant behaves like a true Fungus.

Economic Uses.—*Gigartina mammillosa* (Fig. 264), with cone-like cystocarps 2-5 mm. in length, and *Chondrus crispus* (Fig. 263) with oval cystocarps about 2 mm. long, sunk in the thallus, tetraspores in groups on the terminal segments of the thallus. Both forms occur in the North Sea as purplish-red or purplish-brown Algæ; when dried they have a light-yellow colour, and furnish the official CARRAGHEEN, "Irish Moss," used in the preparation of jelly. AGAR-AGAR, which is used for a similar purpose, is obtained from various *Florideae; Gracilaria lichenoides* supplies the Agar of Ceylon (also called *Fucus amylaceus*), *Eucheuma spinosum* the Agar of Java and Madagascar.

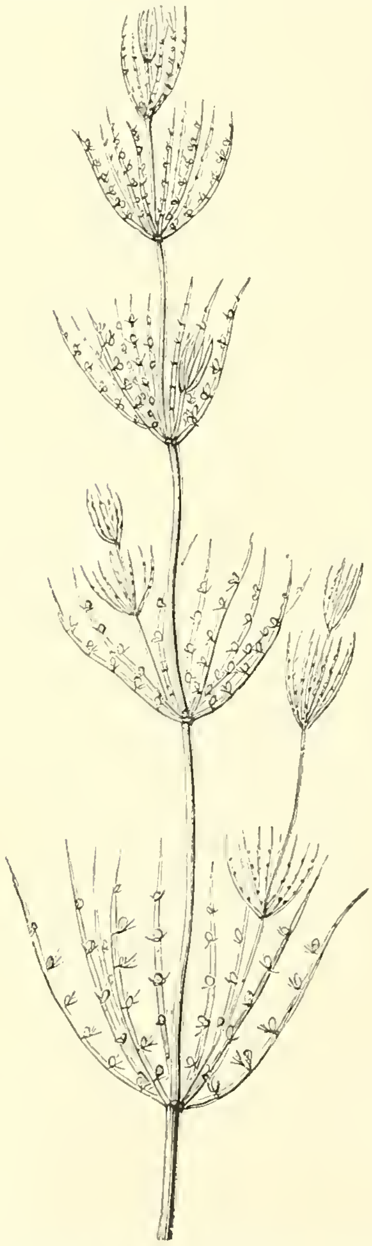


FIG. 268.—*Chara fragilis.* End of main shoot. (Nat. size.)

CLASS XI

Characeae (Stoneworts) (32)

The CHARACEAE, which form a sharply-defined group of Thallophytes, distinctly characterised by the complicated structure of their sexual organs, grow in fresh or brackish water, attached to the bottom and covering extended areas with a mass of vegetation. In some species their cylindrical main axes are over a foot in length, and are composed of long internodes alternating with short nodes, from which short, cylindrical branches are given off in regular whorls with a similar structure, but of limited growth (Fig. 268). The lateral axes are either unbranched or give rise at their nodes to verticillate outgrowths of a second order. From the axil of one of the side branches of each whorl a lateral axis resembling the main axis is produced. The attachment to the substratum is effected by means of branching rhizoid outgrowths from the nodes at the base of the axes.

Both the main and lateral axes grow in length by means of an apical cell, from which other cells are successively cut off by the formation of transverse walls. Each of these cells is again divided by a transverse wall into two cells, from the lower of which a long, internodal cell develops without further division; while the upper, by continued division, gives rise to a disc of nodal cells, the lateral axes, and also, in the lower portion of the main axis, to the rhizoids.

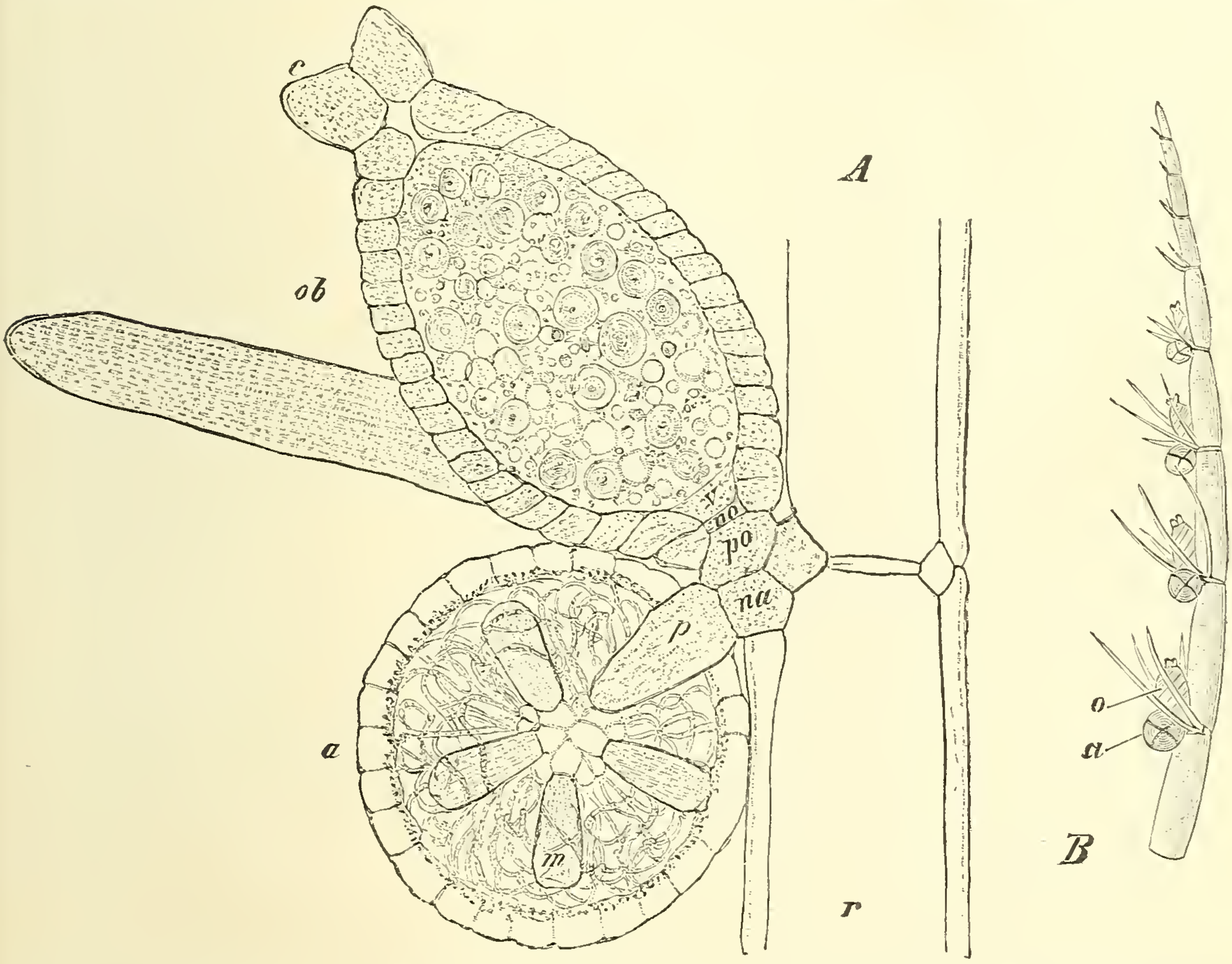


FIG. 269.—*Chara fragilis.* *A*, Median longitudinal section through a lateral axis *r*, and the sexual organs which it bears (× 60); *a*, antheridium borne on the basal nodal cell *na*, by the stalk cell *p*; *m*, manubrium; *ob*, an oogonium; *no*, nodal cell; *po*, the stalk-cell; *v*, pivotal cell; *c*, the crown. *B*, a lateral axis bearing axes of the third order (× 6); *a*, antheridium; *o*, oogonium.

In the genus *Nitella* the long internodes remain naked, but in the genus *Chara* they become enveloped with a cortical layer consisting of longitudinal rows of cells which develop at the nodes from the basal cells of the lateral axes.

As a result of the fragmentation of its original nucleus, each internodal cell is provided with a number of nuclei which lie embedded in an inner and actively moving layer of parietal protoplasm. Numerous chloroplasts are found in the internodal cells.

Asexual reproduction by means of swarm-spores or other spores is unrepresented in the *Characeae*. Sexual reproduction, on the other hand, is provided for by the production of egg-cells and spermatozoids.

The female organs are egg-shaped. They are visible to the naked eye, and, like the spherical red-coloured antheridia, are inserted on the nodes of the lateral axes. With the exception of a few diœcious species, the *Characeae* are monœcious.

The oogonia (Fig. 269, *ob*) contain a large ovum, filled with starch grains and oil-drops; this is surrounded by spirally wound tubular cells forming the envelope. These tubes terminate in the crown (*c*) between slits in which the spermatozoids enter. The antheridia (Fig. 269, *a*) possess a wall formed of eight flat cells with infolded walls, and produce numerous spirally wound spermatozoids. The latter (Fig. 97, *A*) originate from cells composing long filaments which project into the antheridial cavity; they are unlike those of other Algæ and approximate in form to the spermatozoids of the Bryophyta.

The egg, after fertilisation, now converted into an oospore, becomes invested with a thick, colourless wall. The inner walls of the tubes become thickened and encrusted with a deposit of calcium carbonate, while the external walls of the tubes soon become disintegrated; the brown inner walls of the tubes, strengthened by their layer of calcium carbonate, continue as a protective covering after the oospore has fallen from the parent plant.

In a few cases, *e.g. Chara crinita*, the ovum can develop parthenogenetically without being fertilised. Only female examples of this plant occur in Europe.

The oospore, on germination, gives rise first to a simple, filamentous row of cells, the proembryo. From the first node of the proembryo rhizoids are produced, while at the second node there arise, together with a few simple lateral axes, one or more main axes, which finally develop into a full-grown plant.

The formation of tuber-like bodies (bulbils, starch-stars) on the lower part of the axes is characteristic of some species of the *Characeae*. These tubers, which are densely filled with starch and serve as hibernating organs of vegetative reproduction, are either modified nodes with much shortened branch whorls (*e.g.* in *Tolypellopsis stelligera*, when they are star-shaped), or correspondingly modified rhizoids (*e.g.* the bulbils of *Chara aspera*).

CLASS XII

Hyphomycetes (Fungi) ([33, 34])

The *Hyphomycetes* or *Eumycetes* were formerly classified collectively with the *Myxomycetes* and *Schizomycetes* as Fungi. They are, however, quite distinct from each of these classes, and should probably be viewed phylogenetically as representing saprophytic or parasitic forms of the Algæ, in which a complete absence of chlorophyll and chromatophores has resulted from their manner of life. Their cells are provided with distinct but, in most cases, very thin walls, which contain chitin, and have numerous small nuclei dispersed throughout their colourless protoplasm (Fig. 62). In the cell contents are frequently found fat globules and also glycogen, but never true starch. Of all the *Hyphomycetes* the group of the *Phycomycetes*—the

Water or Algal Fungi—although occupying the lowest position, exhibit the most evident connection with the *Chlorophyceae.* Their resemblance to the *Siphoneae*, in particular, is especially pronounced, as their filamentous, vegetative thallus consists of a single, simple, or profusely branched multinuclear cell. The thallus of the higher *Hyphomycetes* is similarly formed of much-branched filaments, but the filaments are septate, and so consist not of one cell but of a row of cells. The filaments, whether septate or unseptate, composing the thallus of the Fungi are termed HYPHÆ; the whole vegetative portion of the thallus formed by them, the MYCELIUM. The hyphæ of a mycelium are, as a rule, either isolated or only loosely interwoven; they spread through the substratum in all directions in their search for organic nourishment. In many of the higher Fungi, however, the profusely and irregularly branching hyphæ become so inseparably knotted and interwoven, that they seem to form compact masses of tissue. Where the filaments in such cases are in intimate contact and divided into short cells, an apparently parenchymatous tissue or PSEUDO-PARENCHYMA is produced. Such compact masses of hyphal tissue are formed by some species of Fungi when their mycelia, in passing into a vegetative resting stage, become converted into SCLEROTIA, tuberous or strand-like, firm, pseudo-parenchymatous bodies, which germinate under certain conditions (Fig. 106). In the fructifications of the higher Fungi the hyphæ are also nearly always aggregated into a more or less compact tissue (Fig. 105).

The modes of asexual and sexual reproduction found in Fungi are more varied than in any other class of the Thallophytes. A survey of the different types of fructification will at the same time exhibit the characteristics of the three main groups into which the Fungi are divided.

1. In the *Phycomycetes* or Algal Fungi, in which the vegetative mycelium is unicellular, except where reproductive organs are being formed, sexual organs are present. These are either differentiated into oogonia and antheridia and produce oospores, or the two conjugating cells (gametes) are similar and form on fusion a zygospore. Many species, however, exhibit an imperfect sexuality; the male organs may be wanting or conjugation may not occur, and the spores originate parthenogenetically.

Three distinct forms of asexual spores can be distinguished. In most *Phycomycetes* sporangia are formed from terminal cells of definite branches of the mycelium (sporangiophores). The protoplasmic contents of the sporangium divide into numerous spores (endospores). These are liberated as ciliated swarm-spores in the aquatic genera, while in the terrestrial forms the spore possesses a wall and is adapted for dispersion in the air.

Conidia or exospores are found in certain genera which may or may not form sporangia also. They arise by abstriction from the ends of branches of the mycelium which are usually developed as specialised conidiophores. The conidia possess cell walls and are distributed by means of the atmosphere.

The third form of spore, which only occasionally occurs in *Phycomycetes*, is the chlamydospore or gemma. These arise in the most simple way from hyphæ in which transverse divisions occur, and the resulting cells, usually associated in rows, become separated from one another.

2. The large group of *Ascomycetes*, in the wide sense, possesses sexual organs, which in their typical form appear as oogonia (here termed carpogonia) and antheridia. The fertilised carpogonial cell does not, however, become a resting oospore, but undergoes development while still connected with the parent plant. Filaments grow from it, the ends of which become transformed into asci, which are a special kind of sporangium. Here, as in the *Florideae*, a non-sexual generation originates from the fertilised egg-cell.

The ascus (Fig. 276), so characteristic of this group, is as a rule an elongated sporangium in which a definite number of spores (usually eight) is formed by free cell formation. In contrast to the formation of spores in the sporangia of *Phycomycetes*, the cytoplasm of the ascus is not completely used up in the formation of the ascospores.

In most groups of *Ascomycetes* the asci, which originate from the carpogonium, are associated in special fructifications; vegetative filaments of the mycelium take part in the formation of these.

Sexual organs are not at present known in all the groups of *Ascomycetes*. In certain orders they are entirely wanting, perhaps as a result of reduction, so that the asci spring directly from the mycelium.

In many Ascomycetes conidia, or more rarely chlamydospores, are formed asexually before the sexual organs or asci have originated.

3. In the third great group, the *Basidiomycetes* in the wide sense, sexual organs are entirely wanting. The asexual multiplication takes place, not by asci, but by means of conidia, and frequently also chlamydospores; the latter are typically developed in the orders *Ustilagineae* and *Uredineae*. The *Basidiomycetes* are characterised by the mode of formation of their conidia. These arise on basidia (Fig. 288), conidiophores of definite form, consisting of one or four cells, and having a definite number of basidiospores (usually four). A further distinction of the basidia from other conidiophores is afforded by the fact that in their development two nuclei fuse with one another, after which the nuclear divisions giving rise to the basidiospores ensue. Other forms of conidiophore, besides the basidia, may occur in the life-history. The more complex *Basidiomycetes* bear the basidia on special fructifications, the origin of which is, however, not dependent on a sexual process.

The classification of the Fungi is not yet completely determined. Probably the class is not a simple one and will have to be subdivided into independent classes when evidence is forthcoming as to its derivation from distinct orders of Algæ. The *Phycomycetes* appear to be derived from the Green Algæ, the *Ascomycetes* show certain resemblances to Red Algæ, while the connection of the *Basidiomycetes* either with Algæ or with the other Fungi is at present obscure.

O. Brefeld, to whose investigations the extension of our knowledge of the life-histories of many Fungi is due, regards the whole class as a single one. He derives the *Ascomycetes*, the sexuality of which he does not recognise, from the sporangium-bearing *Phycomycetes*, the *Basidiomycetes* on the other hand from the conidium-bearing *Phycomycetes* as two apogamous lines of development. Recent investigations on the sexual organs of *Ascomycetes*, and the demonstration of essential differences between sporangia and asci, are opposed to these views.

Sub-Class I. Phycomycetes (35)

The *Phycomycetes*, the unicellular or non-septate mycelium of which suggests comparison with the *Siphoneae* (*Vaucheria*), are divided into two groups characterised by the nature of their sexual organs. The *Oomycetes* produce oogonia and antheridia; the *Zygomycetes* on the other hand have similar sexual cells, which may possibly have been derived from originally different sexual organs.

Order 1. Oomycetes

The genera included in this order live in part as Saprophytes on decaying plants or animals, in part as parasites in the tissues of the higher plants or on insects.

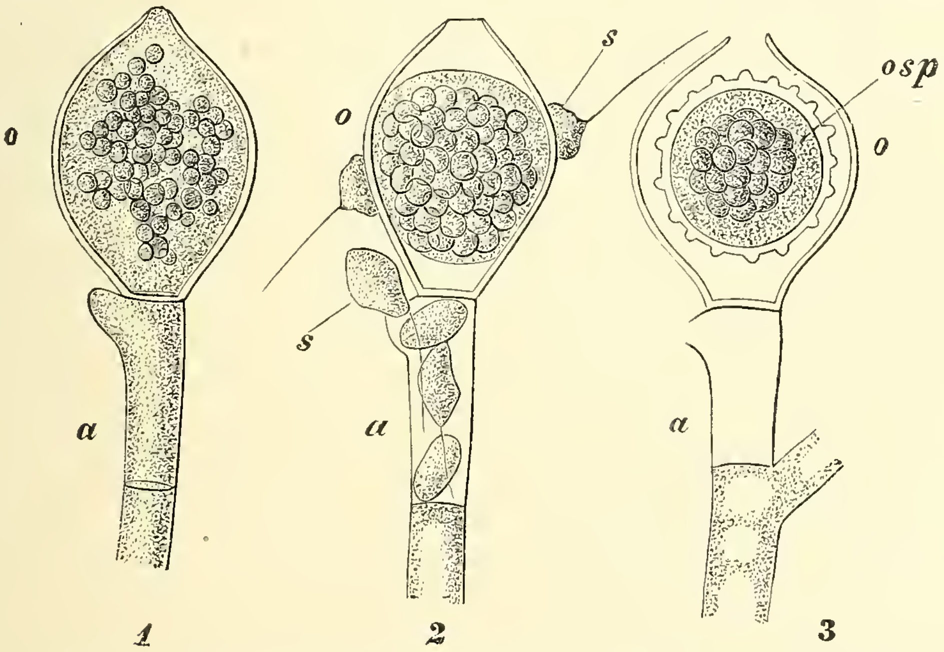


Fig. 270.—*Monoblepharis sphaerica*. End of filament with terminal oogonium (*o*) and an antheridium (*a*): 1, before the formation of the egg-cells and spermatozoids; 2, spermatozoids (*s*) escaping and approaching the opening of the oogonium; 3, *osp*, ripe oospore, and an empty antheridium. (After Cornu, × 800.)

The three families described below are the most important.

1. Only in the small family of the *Monoblepharideae* (36) are free ciliated spermatozoids liberated from the antheridia. In the other *Oomycetes* the multinucleate contents of the antheridium does not divide into separate spermatozoids, but is directly introduced into the egg-cell by means of an outgrowth of the antheridium.

The species of *Monoblepharis* live in water upon decaying organic matter. Asexual reproduction is effected by means of uniciliate swarm-spores, formed in large numbers in terminal sporangia. The sexual organs have the form of terminal oogonia and antheridia borne at the tips of certain hyphæ; the former contain one egg-cell, and the latter numerous uniciliate spermatozoids (Fig. 270). The spermatozoids make their escape through an opening in the antheridium and fertilise the egg-cell, which then becomes transformed into a spinous oospore. In the formation of their sexual organs there is an evident resemblance between the *Monoblepharideae* and the algal genus *Oedogonium* (Fig. 248).

2. The *Saprolegniaceae* (37), which connect on to the preceding family, have a profusely branched mycelium and live in water upon the surface of decaying plants, insects, and even upon living fishes. For the purpose of asexual reproduction they develop terminal club-shaped sporangia, which produce numerous biciliate swarm-spores. In the production of sexual organs, terminal cells of the mycelial hyphæ are converted into spherical oogonia, which give rise to a larger (as many as 50) or smaller number of egg-cells, and less frequently only to one. The antheridia of the *Saprolegnieae* are also tubular, and spring from the hyphæ, usually just below the oogonia. Applying themselves to the oogonia, they send out fertilising-tubes to the egg-cells, which then become converted into thick-walled oospores. In some *Saprolegnieae* no antheridia are formed, and in others they only appear occasionally; in such cases, therefore, the reproduction is parthenogenetic.

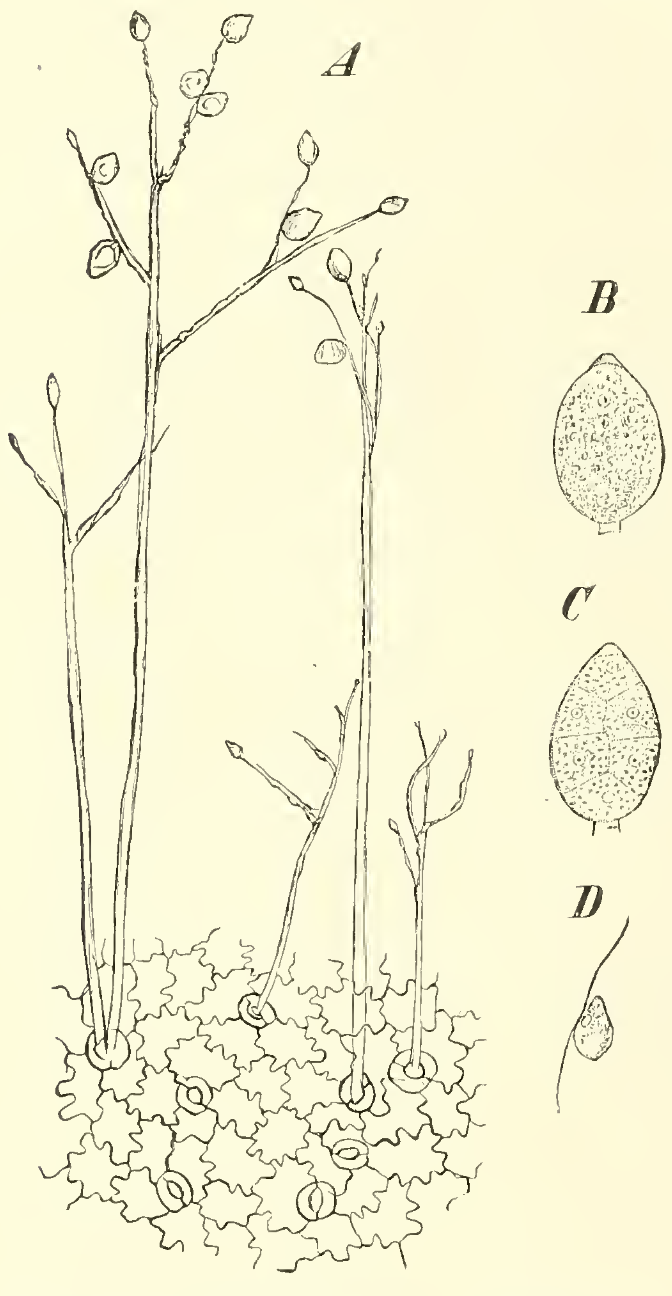


Fig. 271.—*A*, Surface view of the epidermis of a potato leaf, with sporangiophores of *Phytophthora infestans* projecting from the stomata (× 90); *B*, a ripe sporangium; *C*, another in process of division; *D*, a swarm-spore. (*B*-*D* × 540.)

3. The *Peronosporeae* (38) are parasitic Fungi whose profusely branched unicellular mycelium penetrates the tissues of the higher plants, and is frequently the cause of death. In damp climates, certain species occasion epidemic diseases in cultivated plants, and are highly destructive. Thus, the mycelium of *Phytophthora infestans*,

the fungus which causes the Potato disease, lives in the intercellular spaces of the leaves and tubers of the Potato plant, and by penetrating the cells with its short haustoria it leads to the discoloration and death of the foliage and tubers. Sexual reproductive organs have not as yet been observed in this species. Asexual, oval sporangia are formed on long branching sporangiophores which grow out of the stomata, particularly from those on the under side of the leaves (Fig. 271), and appear to the naked eye as a white mould. The sporangia, at first terminal, are cut off by transverse walls from the ends of the branches of the sporangiophore, by the subsequent growth of which they become pushed to one side, and so appear to be inserted laterally. Before any division of their contents has taken place, the sporangia (*B*) fall off and are disseminated by the wind; in this way the epidemic becomes widespread. The development of swarm-spores in sporangia is effected only in water, and is consequently possible only in wet weather. In this process the contents of the sporangium divide into several biciliate swarm-spores (*C*, *D*). Each of these spores after escaping from the sporangium gives rise to a mycelium, which penetrates the tissues of a leaf. The sporangium may also germinate directly without undergoing division and forming swarm-spores: it then has the value of a single spore cut off from a sporophore, and in that case may be regarded as a conidium. A similar transformation of sporangia into conidia is found in other of the *Peronosporeae* as a result of their transition from an aquatic to a terrestrial mode of life.

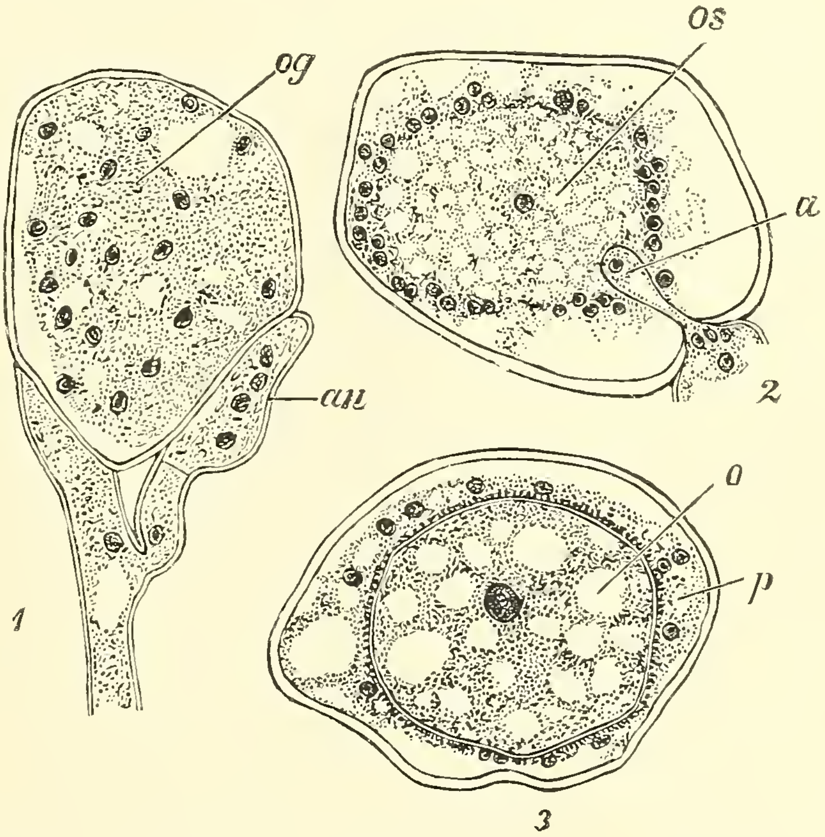


FIG. 272.—Fertilisation of the *Peronosporeae*. 1. *Peronospora parasitica*. Young multinucleate oogonium (*og*) and antheridium (*an*). 2. *Albugo candida*. Oogonium with the central uninucleate oosphere and the fertilising tube (*a*) of the antheridium which contains the male nucleus. 3. The same. Fertilised egg-cell (*o*) surrounded by the periplasm (*p*). (After WAGER. × 666.)

Plasmopara viticola, an extremely destructive parasite, also produces copiously branched sporangiophores and occasions the "False Mildew" of the leaves and fruit of the Grape-vine. *Albugo candida* (= *Cystopus candidus*), another very common species, occurs on *Cruciferae*, in particular on *Capsella bursa pastoris*, causing white swellings on the stems. In this species the sporangia are formed in long chains on the branches of the mycelium under the epidermis of the host plant, and produce numerous swarm-spores.

The sexual organs of the *Peronosporeae* show, in the manner of their formation, a close resemblance to those of the genus *Vaucheria* (Fig. 252). They arise within the host plant—the oogonia as spherical swellings of the ends of certain hyphæ, the antheridia as tube-like outgrowths arising as a rule just below the oogonia. Both are cut off by transverse walls and are multinucleate (Fig. 272). The several species exhibit interesting differences as regards the nuclear changes. In

Peronospora parasitica, *Albugo candida*, and *Pythium* a single large central egg-cell or oosphere becomes differentiated in the protoplasm of the oogonium ; this contains a single nucleus in a central position, while the remaining nuclei pass into the peripheral layer of protoplasm (periplasm). The antheridium now sends a process into the oogonium, which at its apex opens into the oosphere and allows the male nucleus to pass into the latter (Fig. 272, 2). The oosphere then becomes surrounded with a cell wall (Fig. 272, 3), and nuclear fusion takes place, while the periplasm is utilised in forming the outer membrane of the spore (episporium). In *Peronospora parasitica* the ripe oospore has a single nucleus, in *Albugo* it becomes multinucleate as a result of nuclear division. In *Albugo Bliti* and *A. portulacae* there is also a central oosphere surrounded by periplasm, but the oosphere contains numerous nuclei, which fuse in pairs with a number of male nuclei entering from the antheridium. A multinucleate oospore thus arises from the compound egg-cell. *Albugo tragopogonis* occupies an intermediate position in that its oosphere is at first multinucleate, but later contains only one female nucleus, the others having degenerated. The superfluous nuclei in the oogonia and antheridia may be regarded as the nuclei of gametes which have become functionless, and are comparable with the superfluous egg-nuclei of certain *Fucaceae* (cf. p. 331). The oospores either produce a mycelium directly or give rise to swarm-spores.

Order 2. Zygomycetes ([34, 39])

The *Zygomycetes* or *Mucorineae* comprise a number of the most common Mould Fungi. They are saprophytic, and are found chiefly on decaying vegetable and animal substances. Asexual reproduction is effected by non-motile walled spores, which either have the form of conidia or arise endogenously in sporangia. Sexual reproduction consists in the formation of zygospores, as a result of the conjugation of two isomorphous gametes.

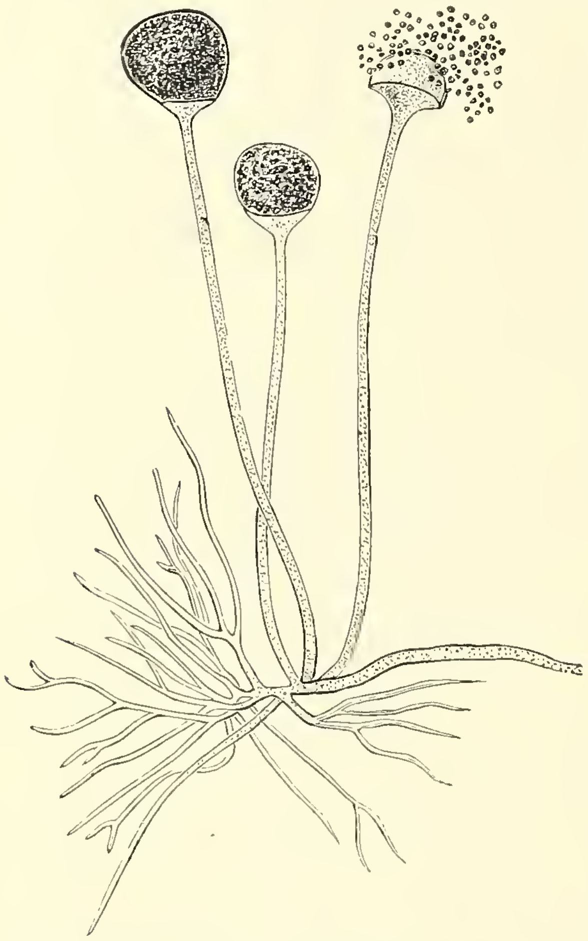


FIG. 273.—*Rhizopus nigricans* (=*Mucor stolonifer*). Portion of the mycelium with three sporangia ; that to the right is shedding its spores and shows the persistent hemispherical columella. (× 38.)

The best known and most widely distributed species is *Mucor Mucedo*, frequently found forming white fur-like growths of mould on damp bread, preserved fruits, dung, etc. *Mucor stolonifer* (=*Rhizopus nigricans*), with a brown mycelium, is similar. The finely-branched mycelium ramifying in the substratum produces a number of erect unbranched sporangiophores (Fig. 273). From the apex of each sporangiophore a single spherical sporangium is cut off by a transverse wall, which protudes into the cavity of the sporangium and forms a columella (Fig. 274, 1, *c*). The contents of the sporangium separate into numerous oval spores embedded in a mass of gelatinous matter capable of great expansion. The wall of the sporangium is easily ruptured, and the spores are discharged by the swelling of the interstitial mass. In *Pilobolus*, which occurs on dung, the sporangium is forcibly cast off from the turgid sporangiophore, which bursts at the columella.

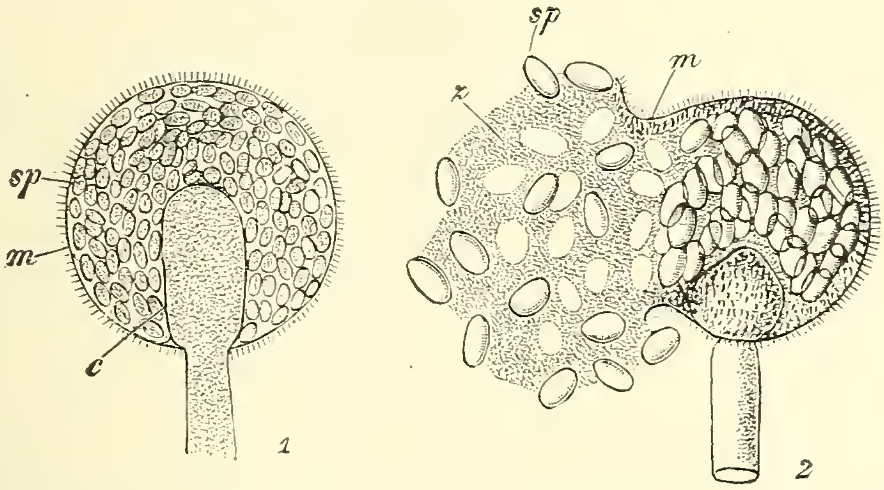


Fig. 274.—1. *Mucor Mucedo.* A sporangium in optical longitudinal section; *c*, columella; *m*, wall of sporangium; *sp*, spores. 2. *Mucor mucilagineus.* A sporangium shedding its spores; the wall (*m*) is ruptured, and the mucilaginous substance between the spores (*z*) is greatly swollen. (After Brefeld, 1 × 225, 2 × 300.) From v. Tavel, Pilze.

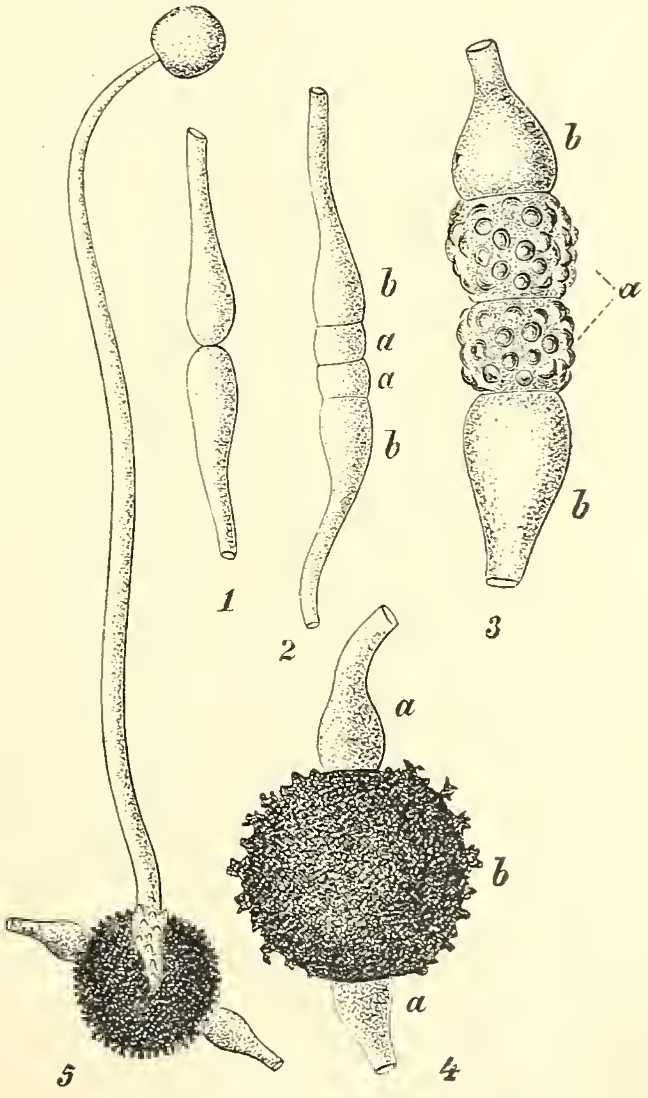


Fig. 275.—*Mucor Mucedo.* Different stages in the formation and germination of the zygospore. 1, Two conjugating branches in contact; 2, septation of the conjugating cells (*a*) from the suspensors (*b*); 3, more advanced stage in the development of the conjugating cells (*a*); 4, ripe zygospore (*b*) between the suspensors (*a*); 5, germinating zygospore with a germ-tube bearing a sporangium. (After Brefeld, 1-4 × 225, 5 × circa 60.)

Under certain conditions, instead of asexual sporangia, organs of sexual reproduction are produced. The hyphæ of the mycelium then give rise to lateral, club-shaped branches. When the tips of two such branches come into contact, a conjugating cell or gamete is cut off from each by a transverse wall (Fig. 275). The two cells thereupon coalesce, and fuse into a ZYGOSPORE, the outer wall of which is covered with warty protuberances. After a period of rest the zygospore germinates, developing a germ-tube, which may at once bear a sporangium (Fig. 275, 5). Both the gametes and the zygospore are, at least in the genus *Sporodinia* according to GRUBER, multinucleate. The behaviour of the nuclei in conjugation is unknown.

Within the group of the *Zygomycetes* also, a reduction of sexuality is perceptible. Thus, in the case of certain *Mucorineae*, although the conjugating hyphæ meet in pairs, no fusion takes place, and their terminal cells become converted directly into spores, which are termed AZYGOSPORES. In other forms again, hyphæ producing azygospores are developed, but remain solitary, and do not, as in the preceding case, come into contact with similar hyphæ. There are also many species in which the formation of zygospores is infrequent.

Both the size and number of spores produced in the sporangia of *Mucor Mucedo* are subject to variation. The sporangia of the genus *Thamnidium* are, on the other hand, regularly dimorphous, and a large sporangium containing many spores is formed at the end of the main axis of the sporangiophore, while numerous small sporangia, having but few spores, are produced by its verticillately branching lateral axes. The sporangia may at times develop only a single spore, as the result of certain conditions of food-supply, and in this way assume the character of conidia. This dimorphism is even more complete in the tropical genus *Choanephora*. In this case, in addition to large sporangia, conidia are produced on special conidiophores. There are, finally, Zygomycetes (*e.g. Chaetocladium*) whose only asexual spores are conidia. In this one group of the *Hyphomycetes*, therefore, all transitional forms, from many-spored sporangia to unicellular conidia, are represented.

Sub-Class II. Ascomycetes ($^{33, 31, 40}$)

The production of spores within asci (Fig. 276) is the chief characteristic of the *Ascomycetes*. The mycelium in this group is septate. The young ascus has at first two nuclei; as a result of the fusion of these it becomes uninucleate. This nucleus gives rise by division to eight nuclei, around which the eight spores form by the process of free cell-formation illustrated in Fig. 95. As a rule the spores form a single longitudinal series, and are ultimately forced out of the ascus, which ruptures at its tip, by the swelling of the surrounding protoplasm.

In most *Ascomycetes* more or less complicated fructifications, the Ascus-fruits, are formed, upon or within which the asci are found. These fruits usually arise from a special organ called the carpogonium. In some genera (*Sphaerotheca*, Fig. 277; *Pyronema*, Fig. 281) HARPER has shown that a fertilisation of the carpogonium by an antheridium occurs, as DE BARY had before assumed to be the case. Probably this process will be found to occur in other members of the group, but it is possible that in many Ascomycetes the sexual organs are no longer produced.

Ascogenous filaments which bear the asci on their ultimate ramifications now arise from the carpogonium. Sterile hyphæ which arise from below the carpogonium also take part in the formation of the fructification, forming an investment to it. The two sorts of hypha are, however, clearly distinguishable. In many respects the *Ascomycetes* recall the *Florideae*, in which an asexual generation bearing the carpospores proceeds from the fertilised egg-cell.

The orders of *Ascomycetes* are characterised by the construction of the fructification.

In the *Perisporiaceae* the small, spherical fruits (perithecia) are surrounded by a complete investing layer, on the rupture or rotting of which the spores are set free.

In the *Discomycetes* open cup-, club-, or hat-shaped fructifications (apothecia) are formed; the asci are arranged parallel to one another in a superficial layer termed the hymenium.

In the *Pyrenomycetes* the perithecia are flask-shaped, the asci springing from the base of the cavity.

In the *Tuberaceae* the subterranean, tuberous fructifications are closed.

To these orders must be added the *Exoasci*, in which the asci arise from cells of the mycelium without the formation of any fructification, and the very simple *Saccharomycetes* or Yeast-Fungi. These two groups can be regarded as extremely reduced *Ascomycetes*. On the other hand they are frequently associated with the *Hemiasci* of BREFELD (41), a number of simple forms in which an indefinitely large number of spores arises from the ascus, and placed at the base of the whole class.

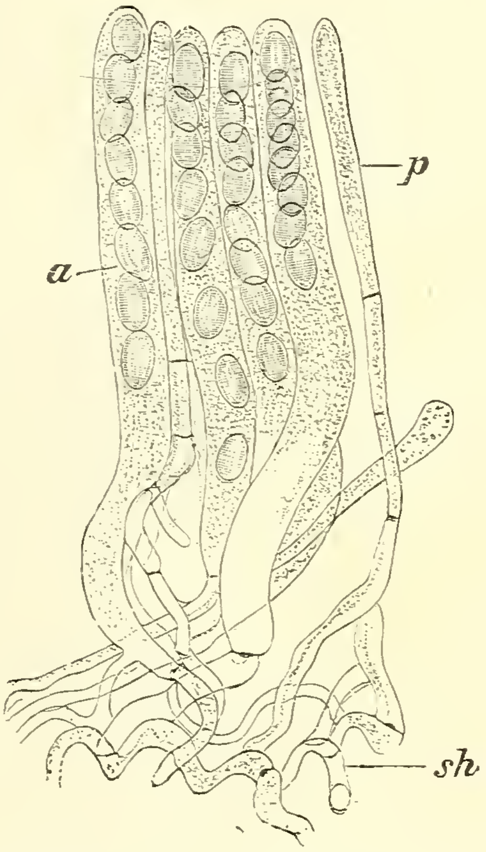


FIG. 276.—Portion of the hymenium of *Morchella esculenta*. *a*, Asci; *p*, paraphyses; *sh*, subhymenial tissue. (× 240.)

The interesting order *Laboulbeniaceae*, which has been accurately investigated by THAXTER (42) should also be mentioned. These are small Fungi, consisting of a few cells, living as parasites on insects; the carpogonium recalls the similarly named organ in the *Florideae*, and like it is fertilised by means of spermatia.

Order 1. Perisporiaceae (33, 43)

This order, which includes only *Ascomycetes* with enclosed fructifications, comprises two families: the *Erysipheae* or Mildew Fungi and the *Perisporieae*.

1. The *Erysipheae* form a family of distinctive epiphytic parasites whose mycelium, somewhat resembling a cobweb, and ramifying in all directions over the surface, particularly the leaves, of higher plants, sends out haustoria which

penetrate the epidermis of the host. The ripe ascus fructifications (perithecia) are black when mature and visible to the naked eye. In the simplest forms (*e.g.* in the genus *Sphaerotheca*) the spheroid perithecium encloses only a single ascus with eight spores. It is enveloped by a covering of sterile hyphæ, forming a sheathing layer, two to three cells deep, of pseudo-parenchyma. The genus *Erysiphe*, on the other hand, develops in each perithecium several asci. The perithecia are irregularly ruptured at their apices and the spores are thus set free. As Harper has shown, the first rudiment of the perithecium consists of an oogonium and an antheridium. These are uninucleate cells, separated from the mycelium by partition walls, and stand close together. The male nucleus passes into the oogonium by an opening which forms in the cell walls (Fig. 277, 1-4.) After fertilisation the oogonium is surrounded by investing filaments which spring from its stalk-cell (5), and the oogonium itself becomes converted into a multicellular structure, the ascogonium (6). In *Sphaerotheca* the ascus containing eight spores arises from the terminal cell of the ascogonium, while in *Erysiphe* this cell produces ascogenous hyphæ which in turn give rise to the numerous asci.

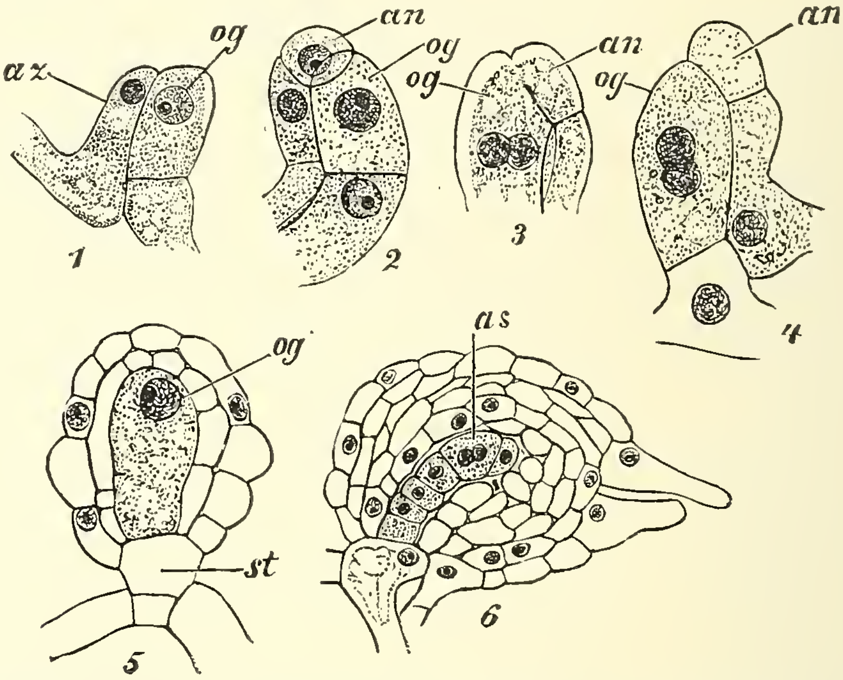


Fig. 277.—*Sphaerotheca castagnei.* Fertilisation and development of the perithecium. 1, Oogonium (*og*) with the antheridial branch (*az*) applied to its surface; 2, separation of antheridium (*an*); 3, passage of the antheridial nucleus towards that of the oogonium; 4, union of the nuclei; 5, fertilised oogonium surrounded by two layers of hyphæ derived from the stalk-cell (*st*); 6, the multicellular ascogonium derived by division from the oogonium; the terminal cell with the two nuclei (*as*) gives rise to the ascus. (After Harper.)

Before entering upon the formation of perithecia, the Mildew Fungi multiply by means of conidia abstricted in chains from special, erect hyphæ, from the tip downwards. The Mildew Fungus of the Grape-vine, *Erysiphe Tuckeri*, exhibits only such conidial fructifications; its ascus-fruit has not as yet been found in Europe. Its conidial form is known as *Oidium Tuckeri*.

2. The *Perisporieae* are closely related to the *Erysipheae*, but are saprophytic and live on decomposing organic matter. To this order belong two of the most common Mould Fungi, *Eurotium herbariorum* and *Penicillium glaucum*. Both at first multiply extensively by means of conidia before they begin to form perithecia.

In the case of *Eurotium herbariorum*, the conidia are abstricted in chains from a number of sterigmata arranged radially on the spherical, swollen ends of the conidiophores (Fig. 278). The conidiophores are closely crowded together, and constitute the white mould, afterwards turning to a blue-green. The Fungus is frequently found on damp vegetables, fruit, bread, etc.

Penicillium crustaceum also forms a very common blue-green mould, particularly on bread. The erect conidiophores constituting the mould are, in this case, verticillately branched and bear at the extremities of each branch flask-shaped cells, from which the chains of conidia are abstricted (Fig. 278).

Spherical perithecia of *Eurotium* and *Penicillium* are produced later on the mycelium, but in the case of the latter genus they are only rarely found. They are of a much more complicated structure than in the *Erysipheae.* They first appear as spirally-coiled fertile hyphæ, which soon (after fertilisation ?) become enveloped by other sterile hyphæ. Entirely enclosed by a tissue of pseudo-parenchyma, the ascogenous hypha gives rise to branches penetrating the pseudo-parenchyma of the perithecial envelope and producing numerous asci containing eight small round spores. In the ripe ascus-fruit the walls of the asci become disorganised and also the investing pseudo-parenchyma, except the outermost layer, which, by suddenly bursting, releases the spores.

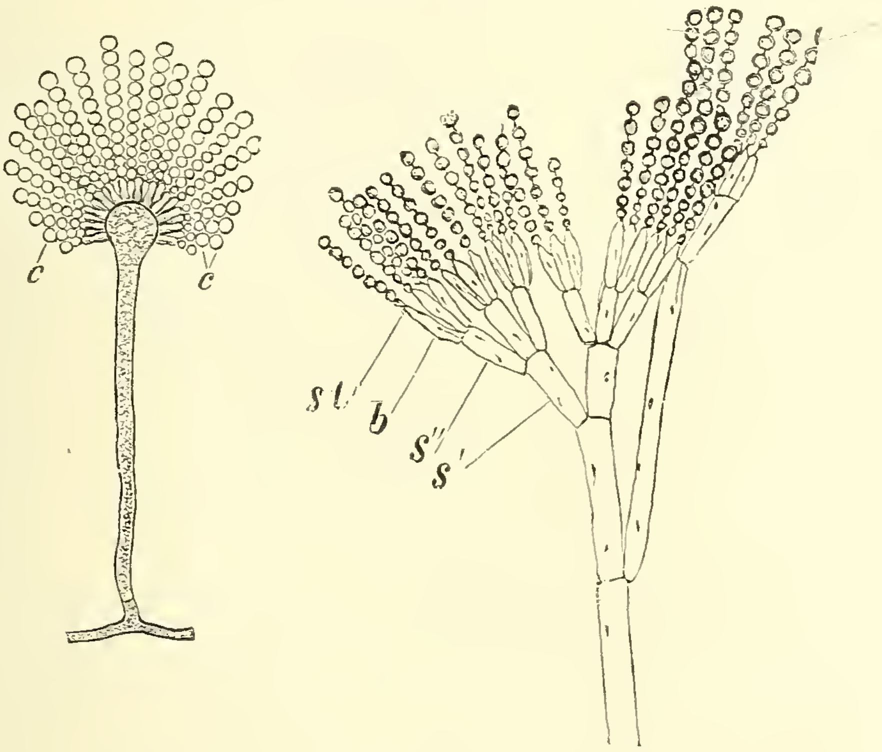


FIG. 278.—Conidiophores of *Eurotium herbariorum* (to the left) and *Penicillium crustaceum* (to the right).

Order 2. Discomycetes (33, 44)

The *Discomycetes* are distinguished from the other orders by their open gymnocarpous apothecia, which bear the hymenium, consisting of asci and paraphyses, freely exposed on their upper surface (Fig. 280). The different groups exhibit great diversity as regards the manner of development of their fructifications.

The great majority of the Discomycetes, of which the genus *Peziza,* with some hundred species, may serve as a type, grow on living or dead vegetable substances, especially upon decaying wood, but sometimes also on humus soil. They produce saucer-, bowl-, funnel-, or disc-shaped fructifications of a fleshy or leathery consistence, and usually of small dimensions. One of the largest forms, *Peziza aurantiaca* (Fig. 279), has seven centimetre-broad, irregularly bowl-shaped fructifications, which are of a bright orange-red colour, while in most of the other species they are gray or brown. Such cup-shaped fructifications are termed APOTHECIA.

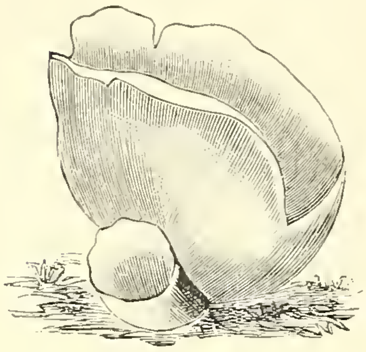


FIG. 279.—*Peziza aurantiaca.* (After KROMBHOLZ, nat. size.)

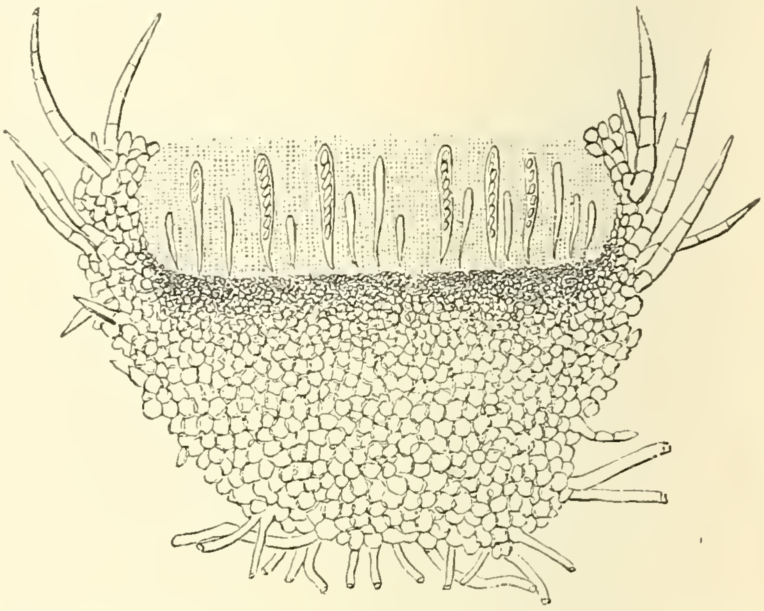


FIG. 280.—*Lachnea pulcherrima.* Apothecium ruptured, showing old and young asci between the paraphyses. (After WORONIN, from v. TAVEL.)

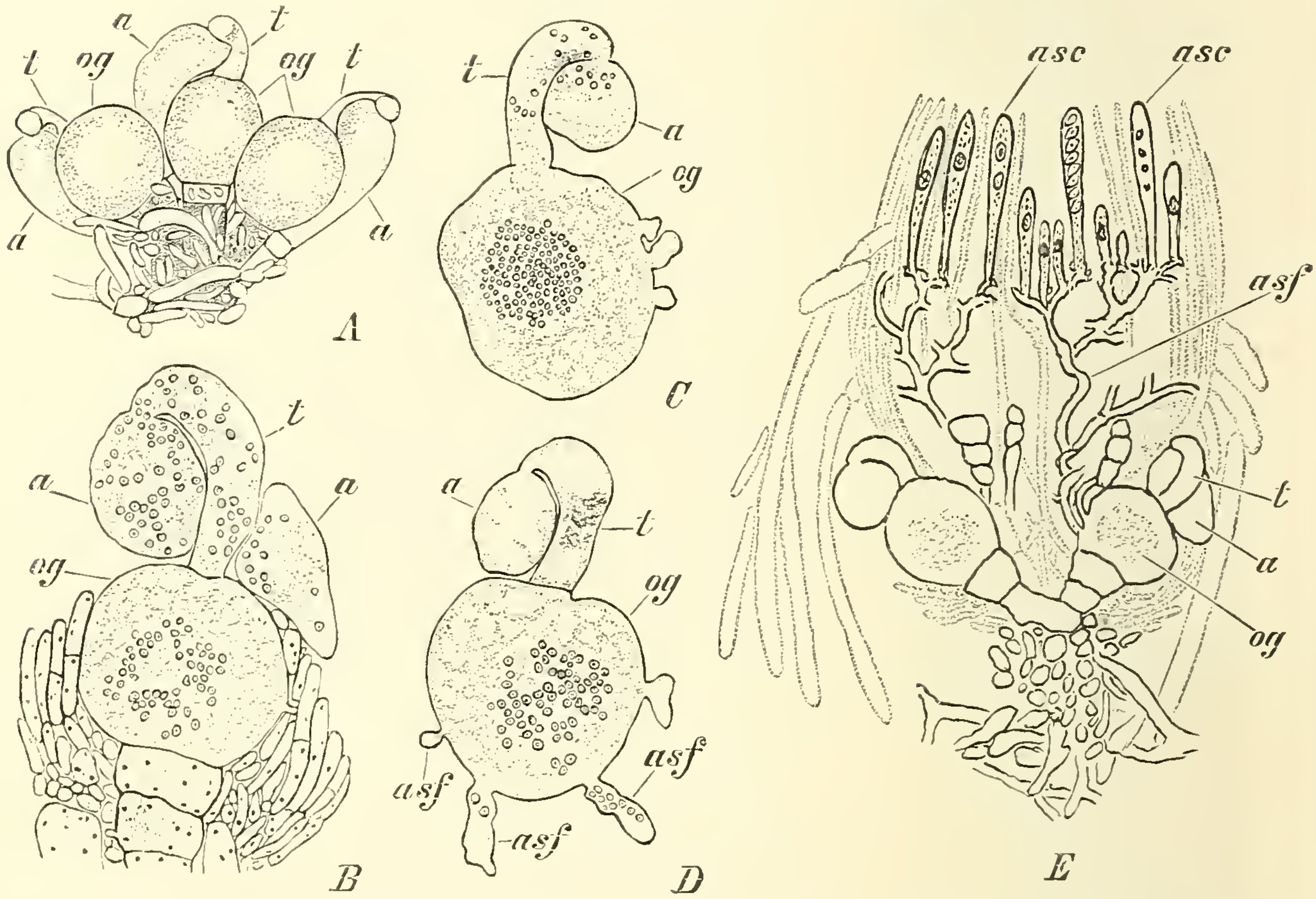


FIG. 281.—*Pyronema confluens.* *A*, Rudiment of an apothecium, consisting of three oogonia (*og*), with trichogynes (*t*) and three antheridia (*a*). *B*, Fusion of the antheridium and the tip of the trichogyne. *C*, The basal-wall of the trichogyne having been absorbed, the male and female nuclei are grouped in the centre of the oogonium. *D*, Separation of the oogonium from the trichogyne by means of a new partition wall. Formation of the ascogenous filaments (*asf*). *E*, Longitudinal section through a young apothecium. *asc*, Asci. (After R. HARPER. *A*, *E*, × about 150, *B*-*D* × about 300.)

The development of the apothecium may be described for *Pyronema confluens*. in which it has been thoroughly investigated by R. HARPER. The fruit-body of this species is about 1 mm. across, and of a yellow or reddish colour; it often occurs on spots where fires have been kindled in woods. The carpogonia are especially large in this species, and several usually take part in the formation of each apothecium (Fig. 281, *A*). The carpogonium consists of the spherical, multinucleate oogonium, on the apex of which a multinucleate curved cell, the trichogyne, is situated. The cylindrical, multinucleate antheridium arises below the oogonium; its apex comes into open communication with the tip of the trichogyne by the breaking down of the intervening walls. The male nuclei first wander into the trichogyne cell, and then, by the breaking down of the basal wall of the latter, into the oogonium. In the oogonium the male nuclei conjugate in pairs with the numerous female nuclei, while the nuclei of the trichogyne cell disintegrate. The egg-cell then becomes limited from the trichogyne by a new cell-wall and sends out ascogenous filaments containing the conjugated nuclei. These filaments branch and ultimately terminate in asci (*E*), while the sterile hyphæ and the paraphyses of the fructification are derived from hyphæ arising beneath the ascogonium. In this case then the oogonium is converted directly into the ascogonium, while in the *Erysipheae* (Fig. 277) the fertilised ovum is first converted into a multicellular ascogonium. In *Ascobolus*, however, a genus related to *Pyronema*, the ascogonium is to begin with multicellular, but all the cells empty their contents into a single large one, from which the ascogenous hyphæ then arise. Considerable variety exists in the structure of the carpogonium and ascogonium; in the Lichen-forming *Ascomycetes* (Fig. 311) another type of carpogonium is found. Further investigations are needed to afford an explanation of these differences.

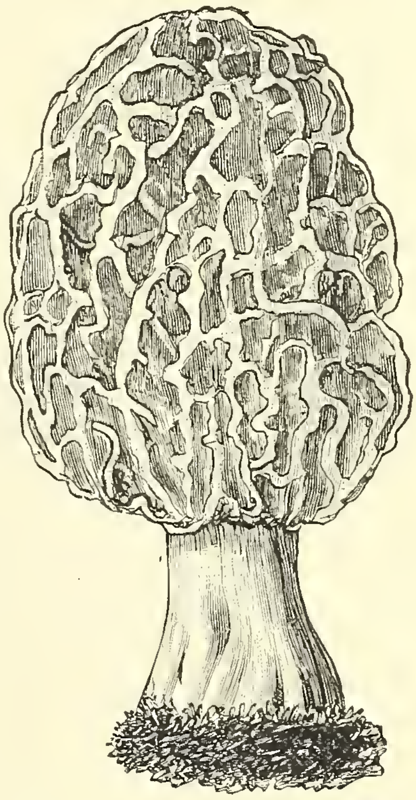


FIG. 282.—*Morchella esculenta.* ($\frac{1}{5}$ nat. size.)

The highest development is exhibited by the peculiar fructifications of the *Helvellaceae* or Morel Fungi, whose mycelium, like that of the Truffle Fungi, vegetates underground in the humus soil of woods, but produces soft wax-like aerial fructifications. In the genus *Morchella*, Morel (Fig. 282), the fructifications consist of a thick erect stalk, bearing a club-shaped or more or less spherical cap or pileus, which bears the hymenium, with its eight-spored asci, on the reticulately indented exterior surface (Fig. 276). The Morchellas are edible ([45]), in particular *M. esculenta* and *M. conica.* The former has a yellowish-brown cap, ovately spherical in shape, and attains a height of 12 cm.; the cap of the latter is conical and dark brown, and it reaches a size of 15 cm. *Gyromitra esculenta*, with dark brown cap and white stalk, and others are also edible. In their external appearance the fructifications of these highly-developed *Discomycetes* greatly resemble those of the *Basidiomycetes.*

Order 3. Pyrenomycetes

The Pyrenomycetes comprise an exceedingly varied group of Fungi, some of which are parasitic upon different portions of plants, particularly on the cortex and leaves, and others are saprophytic upon decaying wood, dung, etc., while a few genera occur as parasites upon the larvae of insects. The flask-shaped fructifications or perithecia are characteristic of this order. The perithecia are open at the top, and are covered inside, at the base, with a hymenial layer of asci and hair-like paraphyses (Fig. 283). The lateral walls are coated with similar hyphal hairs, the paraphyses. The spores escape from the perithecia through the aperture. In this process one ascus after another elongates in consequence of the water absorbed, and discharges its spores through the opening, or the spores are set free within the perithecia, and are ejected, embedded in a swollen mass of slime.

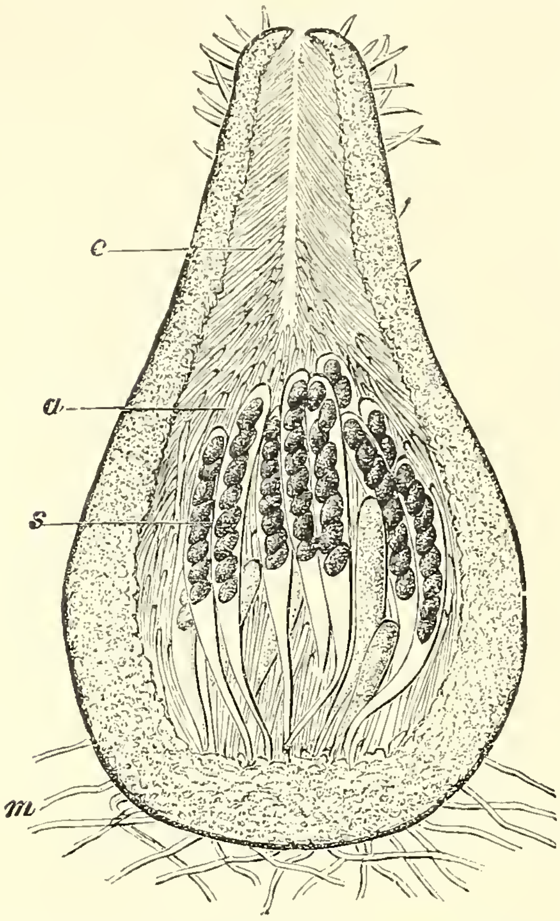


FIG. 283.—Perithecium of *Podospora fimiseda* in longitudinal section. *s*, Asci; *a*, paraphyses; *e*, periphyses; *m*, mycelial hyphæ. (After V. TAVEL, × 90.)

The simplest *Pyrenomycetes* possess free perithecia (Fig. 283) growing singly on the inconspicuous mycelium, having the appearance of small black dots irregularly disposed over the surface of the organic substratum (*e.g.* *Sphaeria* and *Podospora*). In other cases the formation of the fructifications is more complicated; they arise in groups embedded in a cushion- or club-shaped, sometimes branching, mass of compact mycelial hyphæ having a dense pseudo-parenchymatous structure. Such a fructification is known as a STROMA.

In the life-history of most *Pyrenomycetes* the formation of perithecia is preceded by the production of various accessory fructifications, particularly of conidia, which are abstricted in different ways, either directly from the hyphæ or from special conidiophores, and are especially efficacious in disseminating the Fungi. The conidiophores are frequently united in a conidial stroma in the form of incrustations or wart- or club-shaped mycelial masses; they then constitute distinct, conidial fructifications. A special form of such conidia-fruits are the PYCNIDIA produced by many genera. They are small spherical or flask-shaped bodies which in structure resemble the ascogenous perithecia, but, instead of asci, they give rise to branched hyphal filaments from the apices of which conidia, in this case termed PYCNOSPORES or PYCNOCONIDIA, are abstricted (Fig. 284, 1, 2). The different kinds of fructifications in the *Pyrenomycetes* usually make their appearance in succession.

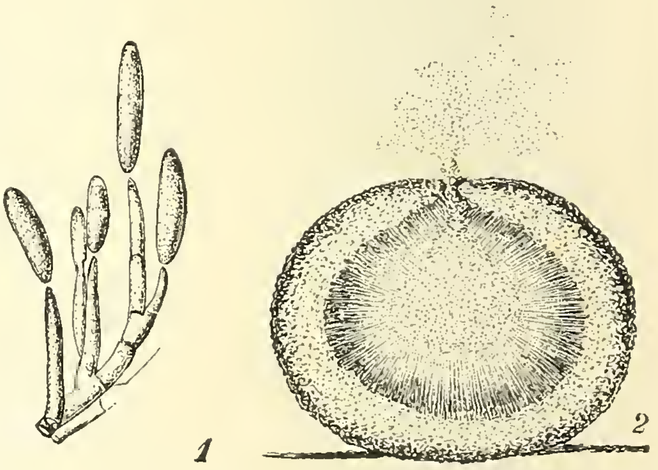


FIG. 284.—1, Conidiophore abstricting conidia, from a pycnidium of *Cryptospora hypodermia*. (After BREFELD, × 300.) 2, Pycnidium of *Strickeria obducens* in vertical section. (After TULASNE, × 70.)

Claviceps purpurea, the Fungus of Ergot, is important on account of its officinal value. It is parasitic in the young ovaries of different members of the *Gramineae*, particularly of Rye. The ovaries are infected in early summer by the ascospores; they become overgrown with the hyphal filaments, and in consequence are deformed. The mycelium soon begins to form conidia, which are abstricted in small clusters from short lateral conidiophores (Fig. 285, *A*). At the same time copious exudations of sweet fluid are extruded. This so-called HONEY-DEW is eagerly sought by insects, and the conidia embedded in it are thus carried to the ovaries of other plants. The conidial form of this Fungus was formerly regarded as a distinct genus under the name of *Sphacelia segetum*. After the completion of this form of fructification, and the absorption of the tissue of the ovary by the mycelium, a

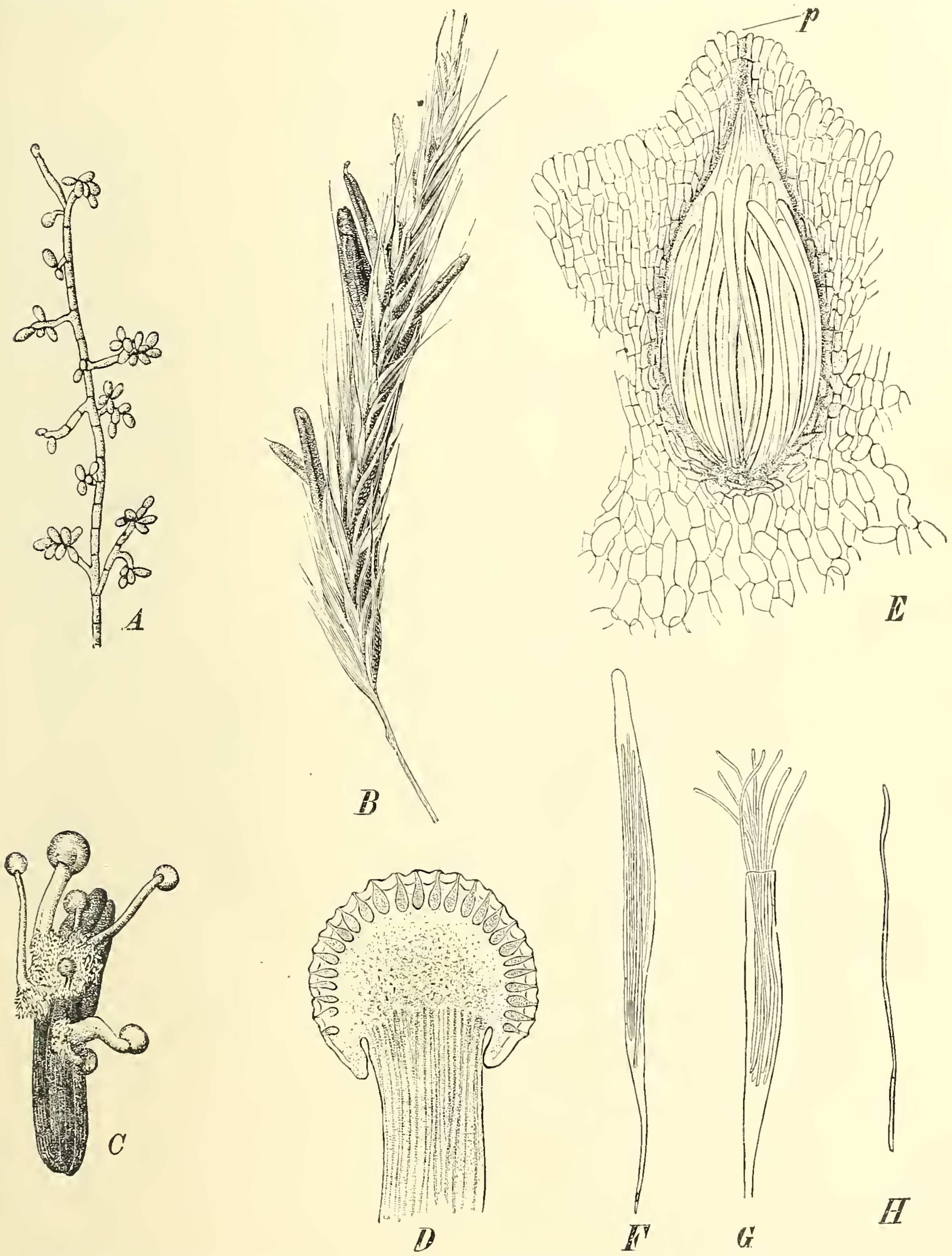


FIG. 285.—*Claviceps purpurea*. *A*, Mycelial hypha with conidia; *B*, ear of Rye with several ripe sclerotia; *C*, a sclerotium with stromata; *D*, longitudinal section of a fructification showing numerous perithecia; *E*, a single perithecium, more highly magnified; *F*, ascus with eight filiform spores; *G*, a ruptured ascus with escaping spores; *H*, a single spore. (*A* after BREFELD; *C-H* after TULASNE; *B* photographed from nature. *OFFICINAL* and *POISONOUS*.)

sclerotium is eventually formed in the place of the ovary from the hyphæ of the mycelium by their intimate union, especially at the periphery, into a compact mass of pseudo-parenchyma (Fig. 106). These elongated dark-violet SCLEROTIA, which project in the form of slightly curved bodies from the ears of corn, are known as Ergot, *Secale cornutum* (Fig. 285, *B*). The sclerotia, copiously supplied with reserve material (fat), eventually fall to the ground, where they pass the winter, and germinate in the following spring when the Rye is again in flower. They give rise to bundles of hyphæ which produce long, stalked, rose-coloured globular heads (*C*). Over the surface of the latter are distributed numerous sunk perithecia (*D*, *E*). Each perithecium contains a number of asci with eight long,

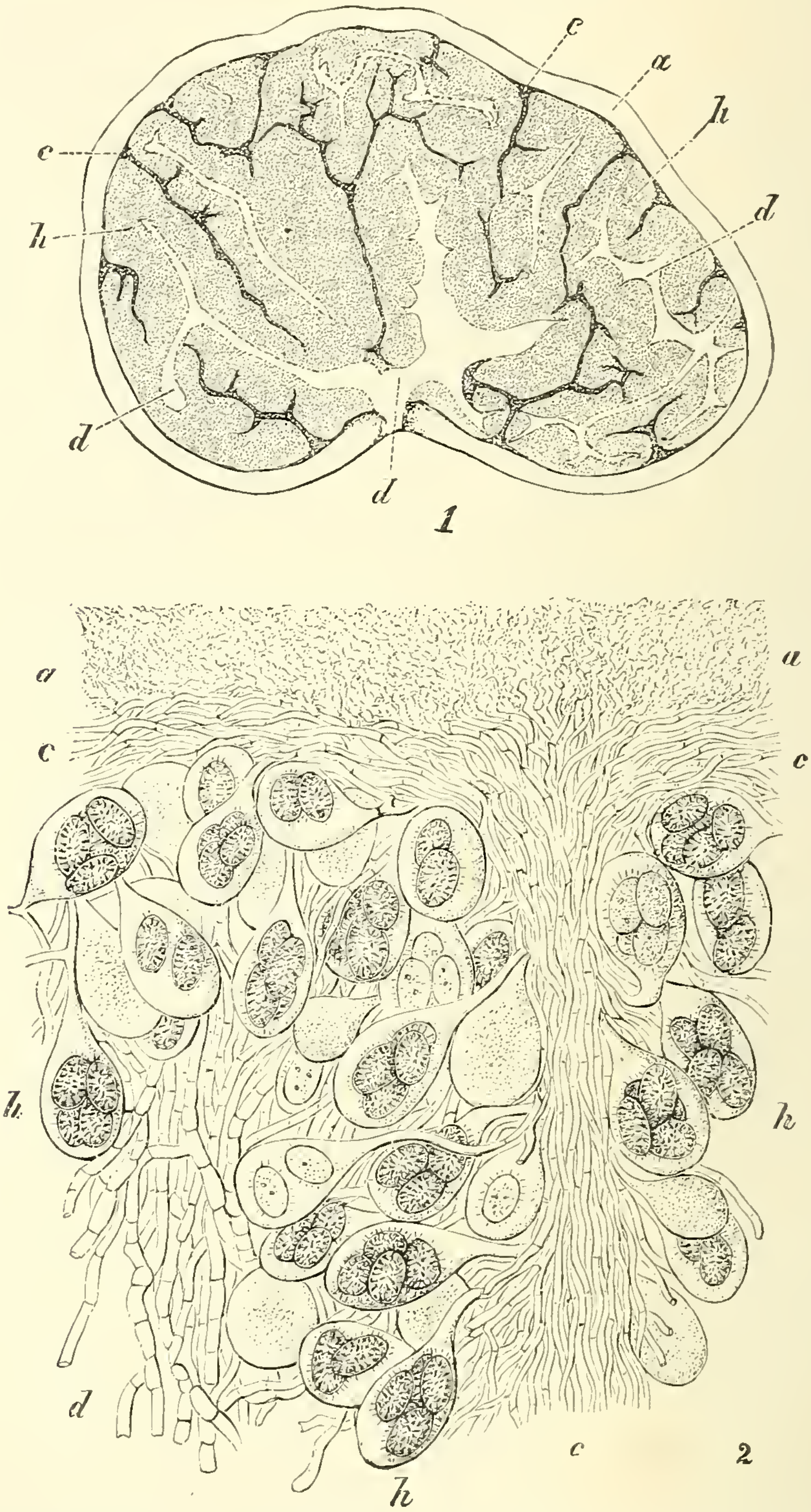


FIG. 286.—*Tuber rufum*. 1, A fructification in vertical section (× 5); *a*, the cortex; *d*, air-passages; *c*, dark veins of compact hyphæ; *h*, ascogenous tissue: 2, a portion of the hymenium. (After TULASNE, from V. TAVEL, × 460.)

filiform ascospores, which are ejected and carried by the wind to the flowering ears of grain.

Officinal.—Secale cornutum (Pharm. germ.) or Ergot is the sclerotium of *Claviceps purpurea.*

Order 4. Tuberaceae (Truffles) (46)

The *Tuberaceae* or Truffle Fungi are saprophytic *Ascomycetes* whose mycelium is entirely subterranean, ramifying in humus soil, particularly in woods under decaying leaves. The ascus fructifications familiar under the name of truffles are underground tuberous bodies (Fig. 286), consisting of a thick, investing, cortical layer, enclosing an inner mass in which the club-shaped asci occur (Fig. 286, 2). The asci contain only a small number of spores; in the case of the true truffles (genus *Tuber*) they are usually only four in number, and generally have a spinous or reticulately-thickened epispore. When the fructifications are fully mature, the sterile tissue in the interior and also the walls of the asci disappear, leaving the ripe spores enveloped only by the outer cortical layer.

The fructifications of many of the *Tuberaceae* are edible (45), and have an aromatic odour and taste. They are, for the most part, obtained from France and Italy. Of the edible varieties, the most important are the so-called black truffles belonging to the genus *Tuber*, viz. *Tuber brumale, melanosporum, aestivum, mesentericum.* The fructifications of these species have a warty cortex of a black, reddish-brown, or dark brown colour. The white truffle, *Choiromyces meandriformis*, is also edible.

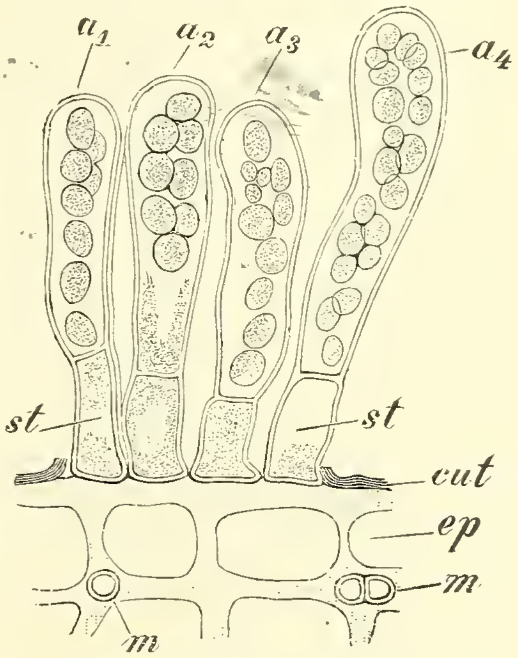


Fig. 287.—*Taphrina Pruni.* Transverse section through the epidermis of an infected plum. Four ripe asci, a_1, a_2 with eight spores, a_3, a_4 with yeast-like conidia abstricted from the spores; *st*, stalk-cells of the asci; *m*, filaments of the mycelium cut transversely; *cut*, cuticle; *ep*, epidermis. (After Sadebeck, × 600.)

Order 5. Exoasci (47)

The most important genus of this group of *Ascomycetes* is *Taphrina* (including *Exoascus*), the species of which are parasitic on various trees. They develop in part annually beneath the cuticle of the leaves, causing discolorations of these organs; their mycelium persists during the winter in the tissue of the host, so that a constant recurrence of the disease takes place. The presence of the mycelium in the tissues of the infected part causes the abnormally profuse development of branches known as Witches'-brooms. *Taphrina Carpini* produces the abnormal growths occurring on the Hornbeam; *Taphrina epiphylla*, those of *Alnus incana. Taphrina deformans* attacks the leaves of the Peach and causes them to curl. *Taphrina Pruni* is parasitic in the young ovaries of many species of *Prunus*, and produces the malformation of the fruit known as "Bladder Plums," containing a cavity, the so-called "pocket," in the place of the stone. In the formation of asci, individual cells of the copiously-branched mycelium ramifying between the epidermis and cuticle of the infected part become greatly swollen. These grow into club-shaped tubes, which burst through the cuticle and, after cutting off a basal stalk-cell, are usually converted into asci with eight spores (Fig. 287). The numerous asci are closely crowded together, and united into a hymenial layer. In consequence of their increased turgor, resulting from an excessive absorption of water, the ascus-tubes become ruptured at their free extremities and eject the spores.

The spores frequently germinate while still enclosed within the asci (Fig. 287, a_3, a_4), and give rise by budding to yeast-like conidia, *e.g.* in *Taphrina Pruni*.

The *Exoasci* are perhaps to be regarded as reduced *Ascomycetes*, from the life-history of which sexuality has entirely disappeared and the sexual organs become completely suppressed.

Order 6. Saccharomycetes (Yeast-Fungi)

The beer, alcohol, and wine yeasts included in the genus *Saccharomyces* are simple unicellular Fungi which assume the form of spherical, oval, or cylindrical conidia containing a single nucleus (Fig. 2). They increase in number by budding. No mycelium is formed, though sometimes the cells remain for a time united in chains. With free access of oxygen and at a suitable temperature Yeasts form sporangia when the nutrient substratum is exhausted ; the sporangia externally resemble the conidia but contain a few spores. Physiologically these Fungi are remarkable for their power of exciting fermentation of saccharine solutions, alcohol and carbon dioxide being produced. The beer yeast is only known in the cultivated form ; the wine yeast, on the other hand, occurs regularly in the soil of vineyards ; the latter is therefore always present on the grapes and need not be added to the grape-juice.

No evidence is at present forthcoming to show that the Yeasts are to be regarded as developmental forms of other Fungi. In various members of the *Mucorineae*, *Exoasci*, and *Ustilagineae*, however, yeast-like conidia which reproduce by budding, are known. Possibly the *Saccharomycetes* are reduced *Ascomycetes*.

Sub-Class III. Basidiomycetes ([34, 45, 48, 49])

The large group of the *Basidiomycetes*, in the wide sense, consists of Fungi, the mycelium of which is septate, as in the *Ascomycetes*. Sexual reproduction is entirely lost. The typical forms are especially characterised by the formation of basidia, or conidiophores of definite shape and size, and bearing a fixed number of spores, usually four (in exceptional cases two, six, or eight). Different forms of basidia are met with.

In the orders *Uredineae* and *Auricularieae* the upper portion of the basidium is divided by transverse walls into four cells ; each cell bears on a thin stalk (sterigma), arising near the upper end, a single spore (Fig. 288, *A*). In the *Tremellineae*, on the other hand, the basidium is divided by longitudinal walls into four cells, each of which continues into a long tubular sterigma (Fig. 288, *B*). The basidium in the *Hymenomycetes* and *Gasteromycetes* is unicellular, and bears as a rule four spores at the summit ; these may be sessile or situated on sterigmata (Figs. 288 *C*, 294). The developing basidium contains two nuclei, which fuse with one another. By the division of the nucleus formed in this way the nuclei of the spores arise.

BREFELD distinguishes the divided basidia as protobasidia, the undivided as autobasidia.

In one family of the *Ustilagineae* the basidia are divided, and not always strictly four-celled; in the other the basidia are undivided. The number of spores produced is not a definite one, but often very large. On this account BREFELD terms these conidiophores, hemibasidia, and groups the forms belonging to this order as *Hemibasidii.* He regards them as preceding the typical *Basidiomycetes,* and among the latter would consider the forms with protobasidia as more primitive than those with autobasidia.

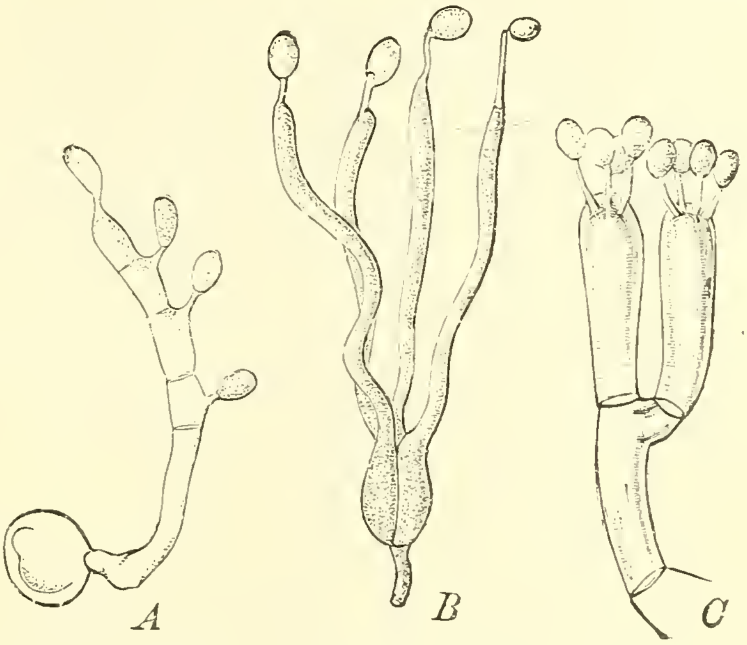


FIG. 288.—Basidia of *Endophyllum Euphorbiae silvaticae* (*A*), *Tremella lutescens* (*B*), and *Tomentella granulata* (*C*), belonging respectively to the orders *Uredineae, Tremellineae,* and *Hymenomycetes.* (*A* after TULASNE; *B, C* after BREFELD, from v. TAVEL; *A, B* × 450; *C* × 350.)

In addition to conidiophores differentiated as basidia, the *Basidiomycetes* produce other forms of conidia as accessory fructifications in many species. Chlamydospores play an important part in the two first orders, appearing in the *Ustilagineae* as the brand spores, and as three forms of rust spore in the *Uredineae.* In these groups the basidia arise directly from the germinating chlamydospores (Figs. 288, *A*, 289, *B*). In other *Basidiomycetes,* if a few simple forms are disregarded, the basidia are always borne upon or within (*Gasteromycetes*) more or less complicated fructifications.

Order 1. Ustilagineae (Brand Fungi) (34, 50)

The *Ustilagineae* are parasites, and their mycelium is found ramifying in higher plants, usually in definite organs, either in the leaves and stems, or in the fruit or stamens. The *Gramineae* in particular serve as host plants for the Brand Fungi, certain species of which are in a high degree injurious to cereals, and produce in the inflorescences of Oats, Barley, Wheat, Millet, and Maize the disease known as smut.

At the end of its period of vegetation the mycelium of the Brand Fungi produces in or upon the host plant the so-called brand spores by the formation of additional transverse walls, and by the division of its profusely branched hyphæ into short swollen cells (Fig. 289, *A*). The cells become rounded off and converted into spores, while their cell walls undergo a mucilaginous modification. The spores thus surrounded by gelatinous envelopes, which, however, eventually disappear, then become invested with a new, thick, double wall, consisting of a thin colourless endosporium and a thick dark-coloured exosporium. In this way the mycelium is transformed into a dark-brown or black mass of spores. As regards the manner of their formation, the brand spores may be regarded as chlamydospores. The brand spores are resting spores, they are scattered by the wind, and germinate only after an interval of rest, producing conidiophores in the succeeding spring, the formation of which is characteristically different in the two families of the Brand Fungi, the *Ustilaginaceae* and the *Tilletiaceae*.

Of the *Ustilaginaceae*, the most important genus is *Ustilago*. *U. segetum* (= *U. Carbo*) causes the mildew and blasting of the inflorescence of Oats, Barley, Wheat. The mycelium penetrates the ovary enclosed by the paleæ, and forms dark-brown dust-like masses of escaping brand spores in the place of the seeds. *U. Maydis* produces on the stalks, leaves and inflorescences of the Maize tumour-like swellings filled with brand spores in the form of a black powder. Other species live on the leaves of different grasses; while *U. violacea* (= *U. antherarum*) occurs in the anthers of various *Caryophyllaceae* (*e.g. Lychnis*), and fills the pollen-sacs with brand spores.

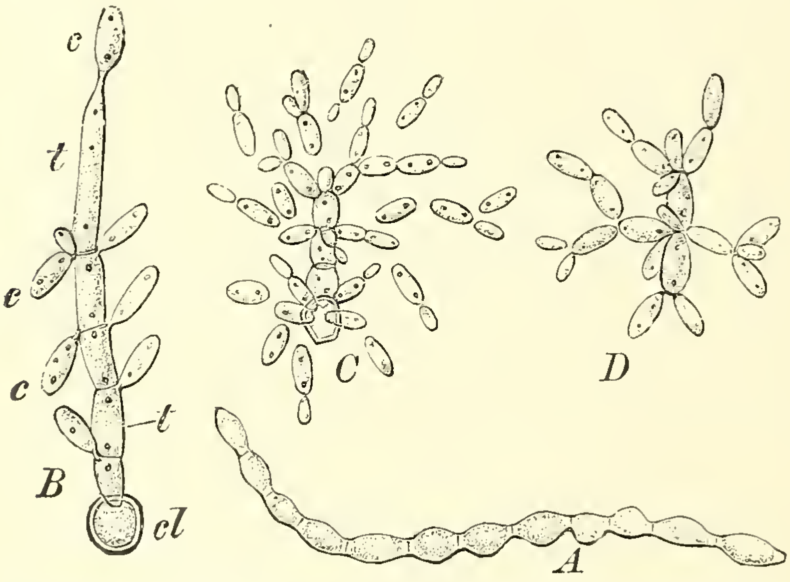


Fig. 289.—*A*, *Ustilago olivacea*. Mycelial hypha in process of forming brand spores (× 400). *B-D*, *Ustilago segetum*: *B*, germinating brand spore; *cl*, cultivated in nutrient solution (× 450); *t*, transversely septate conidiophores with lateral and terminal conidia (*c*): *C*, germinating brand spore lying in the nutrient solution surrounded by abstricted conidia, which are multiplying by budding (× 200): *D*, an aggregation of budding conidia (× 350). (After Brefeld, from v. Tavel.)

The brand spores of *Ustilago* fall to the ground, and after a period of rest give rise, on germinating, to a short tube which becomes septated by three or four transverse walls (Fig. 289, *B*), and functioning as a conidiophore, produces egg-shaped conidia, both laterally from the upper ends of the intermediate cells, and also from the tips of the terminal cell. When abundantly supplied with nourishment, and also on cultivation in a nutrient solution, conidia are continuously abstricted in large numbers (Fig. 289, *C*), and then multiply further by budding in the manner of yeast cells (*C*, *D*). After the food-supply of the substratum is exhausted, the conidia grow out into mycelial hyphæ. The germination of the conidia in the damp manured soil of the grain fields is accomplished during a saprophytic mode of existence, but the hyphal filaments which are eventually produced become parasitic, and penetrate the young seedlings as far as the vegetative cone, where the inflorescence takes its origin. Then the mycelium continues its development, and ultimately terminates its existence by the production of brand spores. No conidia are formed on the host plant itself.

The life-history of the *Tilletiaceae* is similar to that of the *Ustilaginaceae*. The best known species are *Tilletia Tritici* (= *T. Caries*) and *Tilletia laevis*, the Fungi of the stink-brand of wheat. The brand spores of these species are also produced in the ovaries, from which, however, they do not escape, but remain enclosed within them, filling the apparently healthy grains with black brand spores, smelling like decayed fish. In the first-named species the brand spores are provided with a reticulately thickened epispore ; those of *T. laevis*, on the other hand, are smooth-walled. Unlike the *Ustilagin-aceae*, the germ-tube gives rise only at its apex to filiform conidia, which are disposed in a whorl, and consist of four to twelve spores (Fig. 290, 1). The conidia also exhibit the peculiarity that they coalesce with one another in pairs in an H-form. Such cell fusions also occur between germinating conidia of the *Ustilagineae*, but are not accompanied by nuclear fusions. The filiform conidia germinate readily, and produce sickle-shaped conidia at the apex of the germ-tubes. When abundantly supplied with food material, the germ-tubes grow into large mycelia, from which such sickle-shaped conidia are so abundantly abstricted that they have the appearance of a growth of mould. Thus *Tilletia*, unlike *Ustilago*, produces conidia of two forms ; but in other particulars the development of both groups is the same.

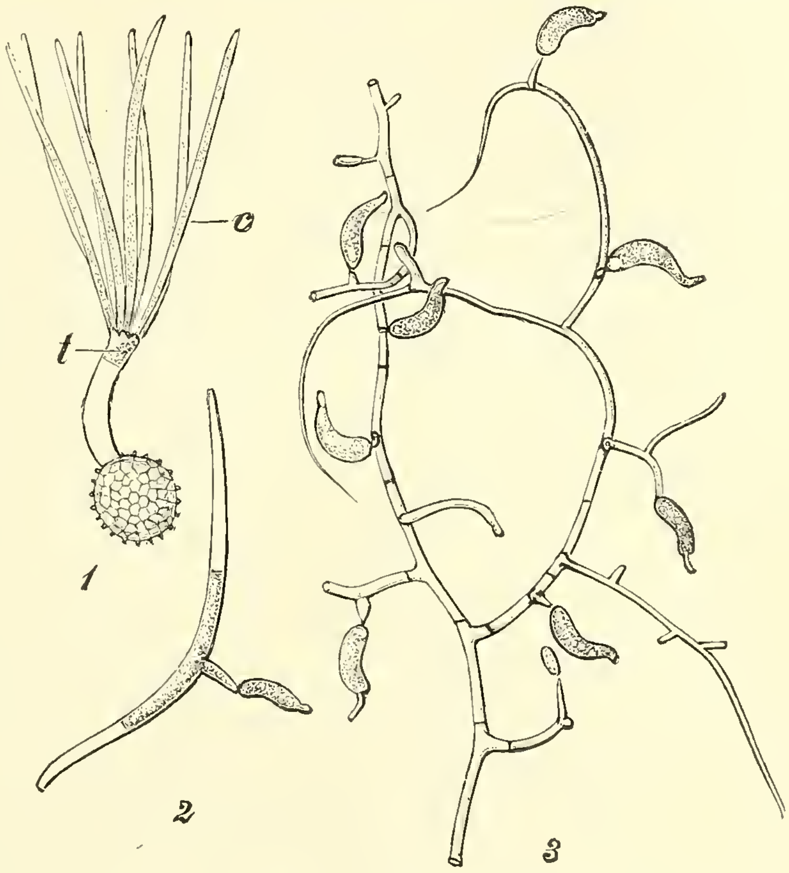


Fig. 290.—*Tilletia Tritici*. 1, Germinating brand spore, with unseptate conidiophore (*t*) and apical filiform conidia (*c*) (× 300) ; 2, a germinating filiform conidium bearing a sickle-shaped conidium (× 400) ; 3, portion of mycelium with sickle-shaped conidia (× 350). (After Brefeld, from v. Tavel.)

Order 2. Uredineae (Rust Fungi) (51)

The Fungi of this order are all injurious parasites. Their mycelium lives in the intercellular spaces in the tissues of the higher plants, particularly in the leaves, which then acquire a spotted, rusty appearance. The Rust Fungi are closely allied to the Brand Fungi. Like them, they produce chlamydospores which break through the tissue of the host and form the rust spots characteristic of these Fungi. The process of chlamydospore-formation, as exhibited by the *Uredineae*, undergoes extensive and complicated modifications ; very frequently three distinct forms of chlamydospore are produced by the same Fungus, at the same time or in succession.

1. The TELEUTOSPORES (winter spores) which, as typical chlamydospores, probably constitute the original form of spores peculiar to all the species, are invested with a thick wall. They are formed at the ends of numerous, closely-clustered mycelial hyphæ which rupture the epidermis in small, usually more or less round spots. They are frequently joined together in rows of two or more (Fig. 292, 1, 5, *t*),

and are produced in late summer, toward the close of the vegetative period. They germinate in the spring and develop at once basidia, bearing four spores (Figs. 288, *A;* 292, 2).

2. The UREDOSPORES (summer spores) arise in the same or similar positions to the teleutospores, but precede them in development. They germinate immediately after their dissemination, producing a vegetative mycelium, and provide for the multiplication of the Fungus during the summer. They are unicellular and enveloped only with a thin wall (Fig. 292, 5 and 6).

3. The ÆCIDIOSPORES, which are produced, prior to either of the other two forms, in special fructifications or ÆCIDIA, germinate, like the uredospores, directly after they have been set free. The æcidia (Fig. 291) are small, at first closed, but afterwards open and cup-shaped bodies; they rupture the epidermis of the host plant, and contain a hymenium of closely-crowded mycelial branches from which chains of round or polyhedral spores are produced by a process of septation. The enveloping layer or PERIDIUM of the æcidia is formed of the peripheral hyphæ, which remain sterile.

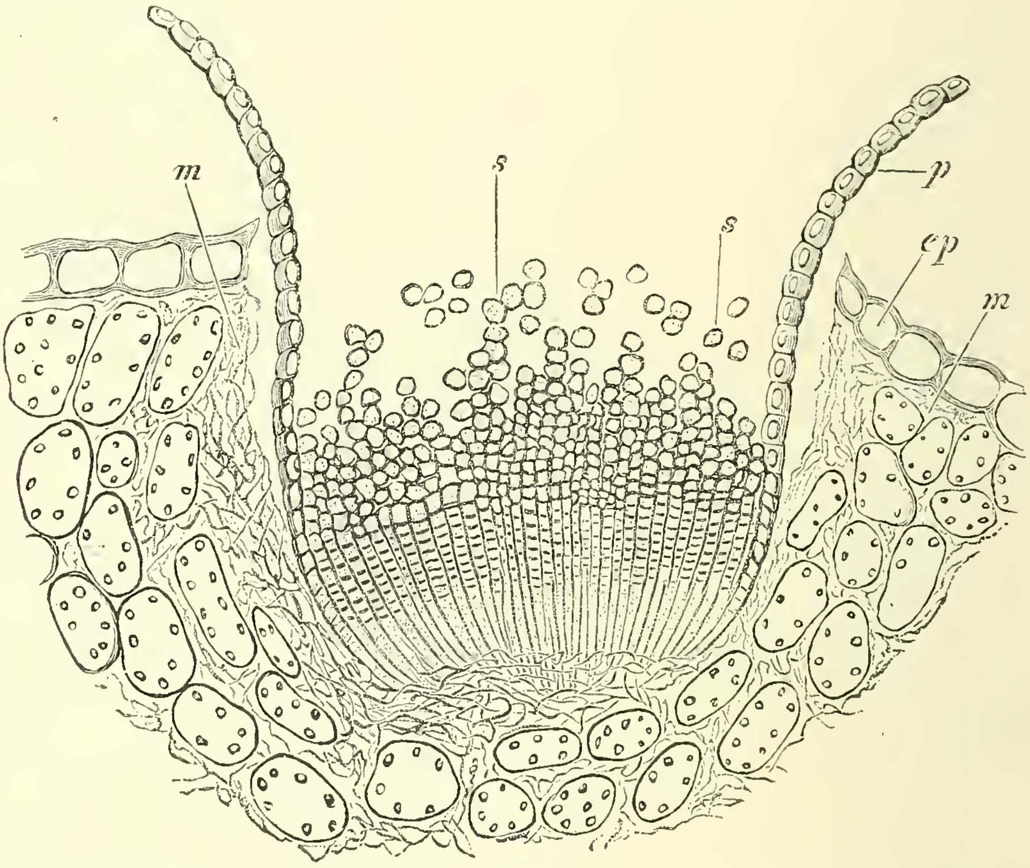


FIG. 291.—*Puccinia graminis.* Æcidium on *Berberis vulgaris;* *ep*, epidermis of lower surface of leaf; *m*, intercellular mycelium; *p*, peridium; *s*, chains of spores. (× 142.)

Uredospores and æcidiospores differ from the teleutospores only in their manner of germinating vegetatively; in the mode of their formation they are to be regarded as chlamydospores, which serve a distinct biological purpose in the dissemination of the Fungus. They have probably been evolved from teleutospores; occasionally transitional forms between teleutospores and uredospores are found.

In the life-history of the *Uredineae* provided with such trimorphous chlamydospores still another asexual sporiferous fructification occurs, resulting in the production of conidia. In this case the conidia are formed in PYCNIDIA similar in form and structure to those exhibited by many of the higher *Ascomycetes.* The pycnidia produce internally minute conidia on filamentous conidiophores, the so-called PYCNOSPORES or PYCNOCONIDIA. The pycnidia were formerly called spermogonia, and the spores, which were thought to be sexual cells, were then termed spermatia.

The pycnoconidia are discharged from the mouth of the spherical or flask-shaped receptacle (Fig. 293); their further development on the host plant is still unknown, but they can be induced to germinate in a nutrient solution. The pycnidia appear in spring with the æcidia, but somewhat earlier, and on the upper side of the leaf, while the æcidia develop on the under side.

The *Uredineae* thus exhibit a great variety of asexual spores, as in addition to the three chlamydospore forms they produce two other kinds of conidia, viz. those formed in the pycnidia and on the basidia. The different spores usually succeed each other, according to the seasons; æcidiospores and pycnoconidia in the spring, uredospores in summer, and teleutospores in autumn, which in the following spring develop basidiospores. The latter germinate at once, and the mycelium penetrates the host plant and produces in turn æcidia, pycnidia, etc. Æcidiospores and

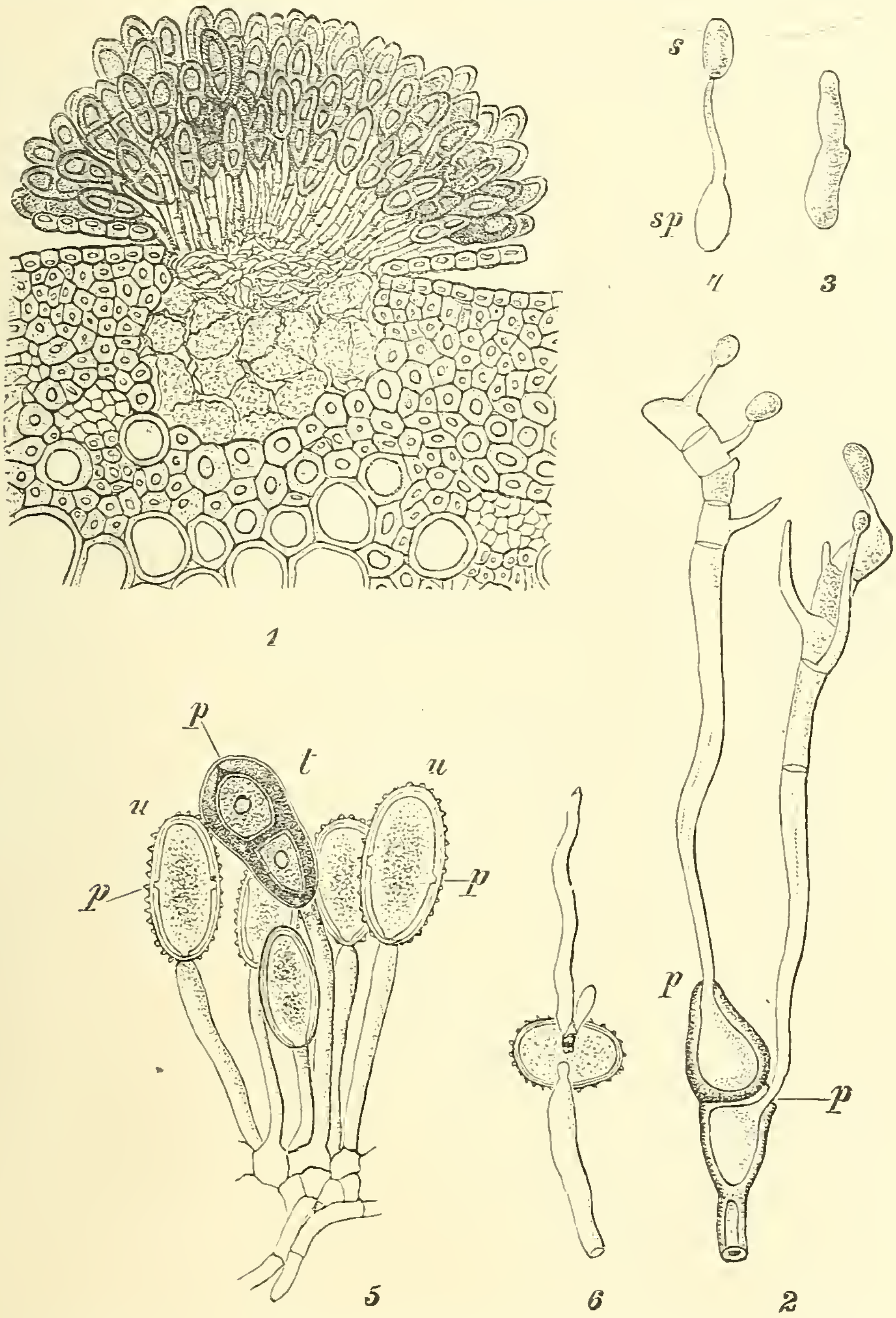


FIG. 292.—*Puccinia graminis*. 1, Transverse section through a grass-haulm with group of teleutospores; 2, germinating teleutospore with two basidia; 3, vegetative, 4, fructifying germinating basidiospore; 5, a portion of a group of uredospores (*u*) and teleutospores (*t*): *p*, the germ-pores; 6, germinating uredospore. (1, 2, 3, 4, after TULASNE; 5, 6, after DE BARY, from v. TAVEL; 1 × 150, 2 × circa 230, 3, 4 × 370, 5 × 300, 6 × 390.)

uredospores provide for the dissemination of the Fungus during the vegetative period.

All the different forms of spores arise in the course of the year, either on the same host plant, or the pycnidia and æcidia may occur on one host plant, and the uredospores and teleutospores on another, often unrelated plant. In the first case the parent Fungi are termed AUTŒCIOUS; in the latter instance they are HETERŒCIOUS, and an alternation of hosts occurs.

An example of an heterœcious Rust Fungus is afforded by *Puccinia graminis*, the rust of wheat. It develops its uredospores and teleutospores on all the green parts of *Gramineae*, especially of Rye, Wheat, Barley, Oats, to which its parasitic mycelium is extremely injurious. The æcidia and pycnidia of this species are found on the leaves of the Barberry (*Berberis vulgaris*). In the spring the hibernating double teleutospores give rise to transversely septate basidia, from which the four basidiospores are abstricted (Fig. 292, 2). These are scattered by the wind, and if they fall on the leaves of the Barberry they germinate at once. The germ-tube penetrates the cuticle, and there forms a mycelium which gives rise to pycnidia on the upper side of the leaf (Fig. 293), and to æcidia on the under side (Fig. 291). This form of the Fungus is known as *Æcidium Berberidis*. On the rupture of the peridium the reddish-yellow æcidiospores are conveyed by the wind to the haulms of grasses, upon which alone they can germinate. The mycelium thus developed produces, particularly on the leaf-sheaths, primarily uredospores (Fig. 292, 5). They are unicellular, studded with warty protuberances, and provided with four equatorially disposed germ-pores. In consequence of the reddish-yellow fat globules contained in the protoplasm of the spores, the fructification forms red markings (formerly termed *Uredo linearis*) on the epidermis of the host plant. The uredospores are capable of germinating at once on the same or other cereals, and thus the rust disease is quickly spread. Towards the end of the summer the same mycelium produces the black, thick-walled teleutospores, which in this species are always double, being united in pairs. Each teleutospore is provided with one germ-pore, and on germination in the succeeding year the cycle is begun afresh.

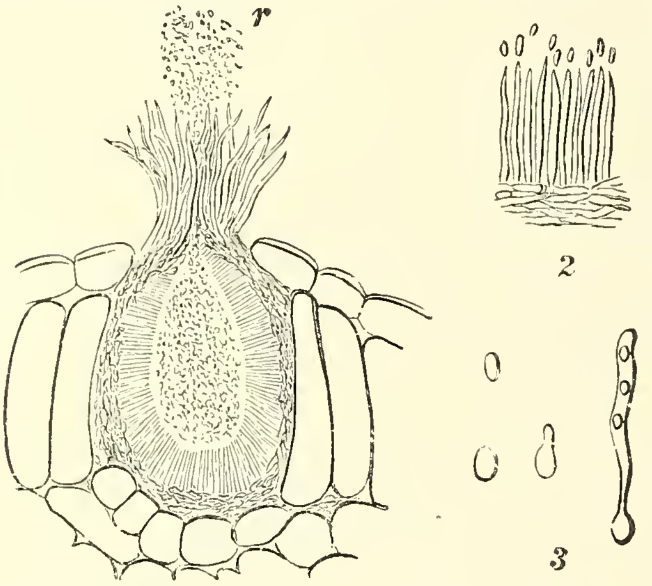


FIG. 293.—*Puccinia graminis*. Transverse section of a leaf of Barberry with a pycnidium in longitudinal section (× 150); *r*, escaping pycnospores; 2, a portion of the hymenium of the pycnidium (× 225); 3, germinating pycnospores with several oil globules shown in the long germ-tube (× 360). (After v. TAVEL.)

The mycelium of the Uredo form may hibernate in winter wheat, and thus the rust may appear in the spring without the previous formation of basidiospores or of æcidia.

Other Rust Fungi, like *Puccinia graminis*, common on *Gramineae*, and having a similar development, are *P. Rubigovera* (= *P. straminis*), with the æcidium form, *Æcidium Asperifolium*, on the *Boragineae*, and *P. coronata*, with the corresponding form, *Æcidium Rhamni*, on *Rhamnus*.

All *Uredineae* do not exhibit so complicated a course of development as *Puccinia graminis*. Certain species produce only basidia from germinating teleutospores, or, in addition to teleutospores, only uredospores which are developed on the same host. Others produce pycnidia and æcidia, and afterwards teleutospores, but no uredospores.

In the case of the heterœcious species, it is only possible to demonstrate the connection between the different spore-forms by means of culture experiments. So long as the relation of the different forms was not known, it was customary to designate each by a special generic name: the Uredo forms as *Uredo;* the Æcidia, according to their structure, as *Æcidium*, *Roestelia*, *Peridermium*, etc. The generic name is now determined by that of the teleutospores, as they exhibit the most characteristic distinctions.

Order 3. Auricularieae

The basidia, as in the case of the *Uredineae*, are transversely septate, with four spores. But few forms are included in this order. Among the most familiar is *Auricularia sambucina* (Judas' ear), found on old Elder stems. It has gelatinous, dark-brown fructifications, which are shell-shaped and bear on their inner sides the basidial hymenium.

Order 4. Tremellineae

The basidia are longitudinally divided (Fig. 288, *B*). The hymenium is situated on the surface of the fructifications, which are generally gelatinous and irregularly lobed or folded. The few genera included in this order are saprophytic on decaying wood and tree-trunks, from whose surface the fructifications are produced.

Order 5. Hymenomycetes

The basidia are undivided, and bear four spores at the apices of slender sterigmata (Fig. 294, *sp*). In the simplest forms these autobasidia spring directly from the mycelium, but in the majority of cases stalked fructifications surmounted by a cup-like expansion, the PILEUS, are produced, which bear definite hymenial layers, composed in addition to the basidia of paraphyses (Fig. 294, *p*), and also of sterile cystids (*c*) or club-shaped tubes characterised by their larger diameter and more strongly thickened wall. In this order, in contrast to the *Uredineae*, the formation of chlamydospores is of rare occurrence, and is correspondingly of subordinate importance.

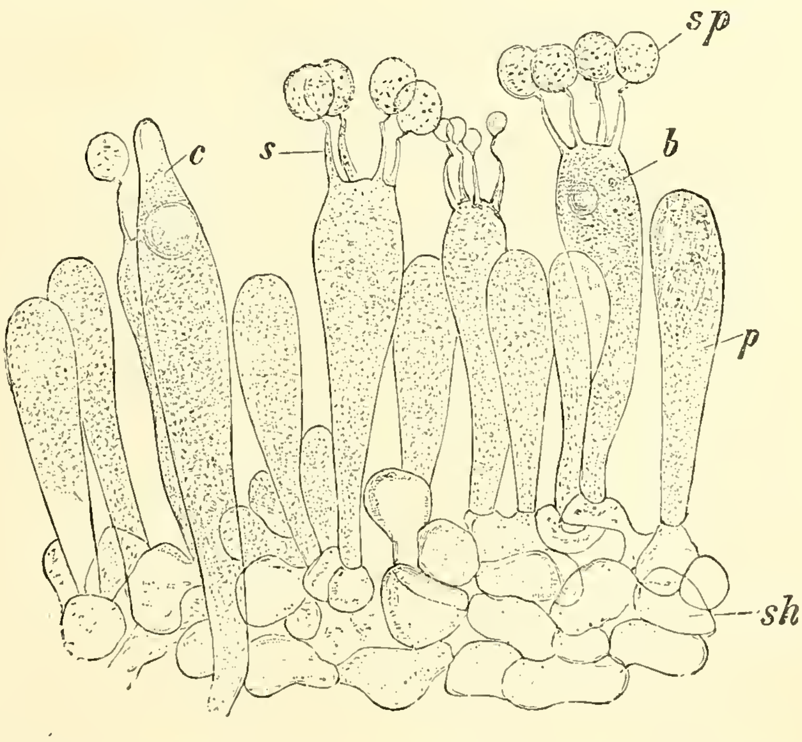


FIG. 294.—*Russula rubra.* Portion of the hymenium. *sh*, Subhymenial layer; *b*, basidia; *s*, sterigmata; *sp*, spores; *p*, paraphyses; *c*, a cystid. (× 540).

Most of the *Hymenomycetes* develop their profusely branched, white mycelium in the humus soil of forests or in decaying wood, and produce fructifications, often of considerable size, protruding from the substratum. The mycelium of the forms vegetating in the soil spreads further and further, and dying in the centre as it exhausts the food material of the substratum, occupies continually widening concentric zones. In consequence of this mode of growth, where the development has been undisturbed, the fructifications which appear in autumn form the so-called fairy rings. A few *Hymenomycetes* are parasitic, and vegetate in the bark or wood of trees. Of such parasitic forms *Armillaria mellea*, whose mycelium vegetates between the bark and wood of Conifers, is a familiar example. The profusely branching mycelial hyphæ undergo a remarkable modification (Fig. 295), and become interwoven into flat, black strands from which fine, hair-like hyphæ are sent out and penetrate the wood for the absorption of nourishment. It is from these strands, known as RHIZOMORPHA, that the stalked, capitate fructifications are eventually produced. In addition to the subcortical strands, subterranean mycelial strands are developed which pervade the soil and infect the roots of other trees. The rhizomorphs may also be regarded as a form of sclerotia.

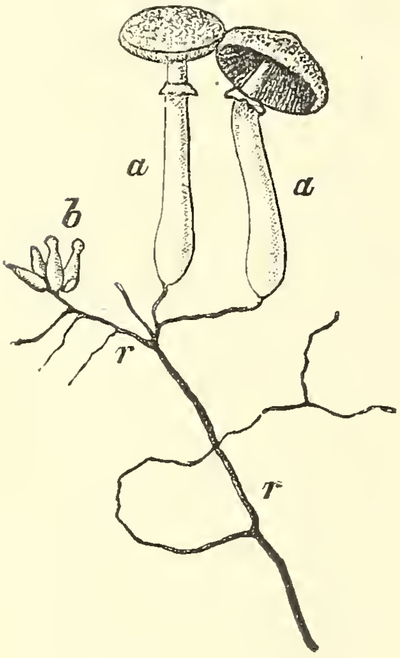


FIG. 295.—*Armillaria mellea.* Portion of a rhizomorpha strand (*r*) with mature (*a*) and young (*b*) fructifications. (After HARTIG, from v. TAVEL ; ½ nat. size.)

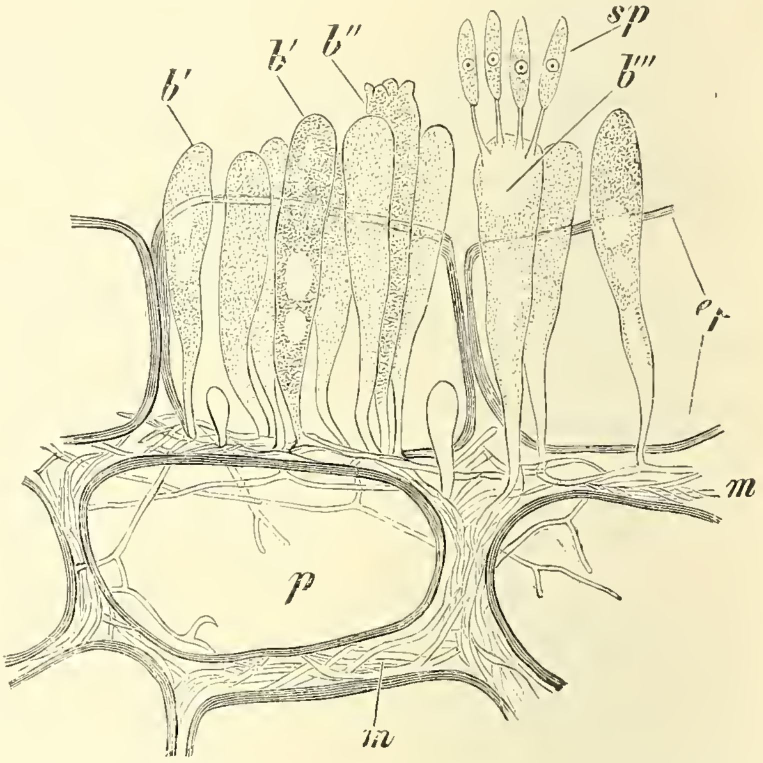


FIG. 296.—*Exobasidium Vaccinii.* Transverse section through the periphery of a stem of *Vaccinium* ; *ep*, epidermis ; *p*, cortical parenchyma ; *m*, mycelial hyphæ ; *b′*, protruding basidia without sterigmata ; *b″*, with rudimentary sterigmata ; *b‴*, with four spores. (After WORONIN, × 620.)

The *Hymenomycetes* are further classified according to the increasing complexity exhibited in the structure of their basidial fructifications.

1. In a few genera no distinctive fructifications are formed, and the autobasidia spring in irregular groups directly from the mycelium. *Exobasidium Vaccinii* (52) may be taken as a type of this form. The mycelium of this Fungus, which is widely spread in Europe, is parasitic in the *Ericaceae*, especially on species of *Vaccinium* ; it causes hypertrophy of the infected parts. The basidia are formed in groups under the epidermis, which they finally rupture (Fig. 296). In this genus, as in many others, accessory fructifications are developed, and as spindle-shaped conidia are abstricted before the formation of the basida from the mycelium on the surface of the host plant.

2. In the group of the *Thelephoreae*, distinctive fructifications of a simple type are found. They are composed of closely interwoven hyphæ, and form on the trunks of trees either flat, leathery incrustations bearing the hymenium on their smooth upper surfaces; or the flat fructifications become raised above the substratum and form bracket-like projections, which frequently show an imbricated arrangement, and bear the hymenium on the under side (*e.g. Stereum hirsutum*, common on the stems of deciduous trees).

3. The fructifications of the *Clavarieae* form erect whitish or yellow-coloured bodies, either fleshy and club-shaped or more or less branched, resembling coral (*Clavaria*, Fig. 297). The larger profusely branched forms of this group are highly esteemed for their edible qualities; in particular, *Clavaria flava*, whose fleshy, yellow-coloured fructifications are often ten centimetres high, also *Clavaria botrytis* (Fig. 297) and *Sparassis crispa*, which grows in sandy soil in Pine woods, having fructifications half a metre thick, with compressed leaf-like branches.

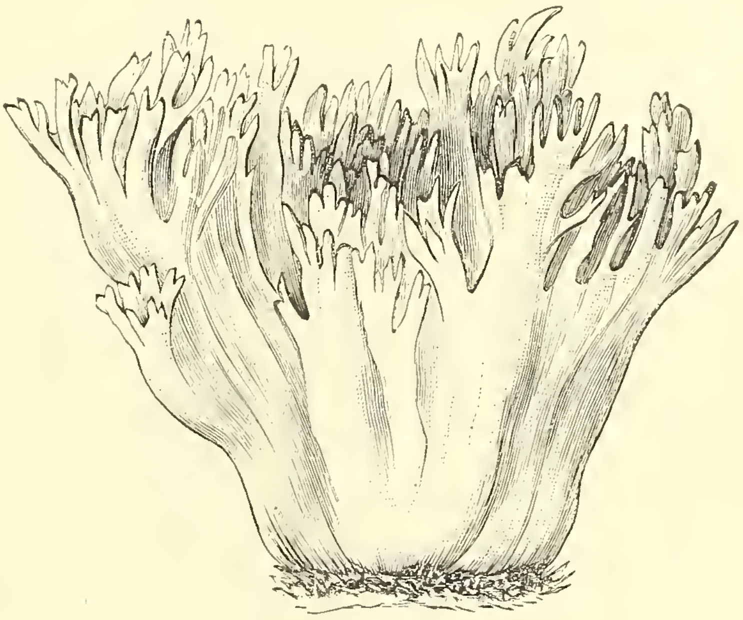


FIG. 297.—*Clavaria botrytis*. (Nat. size.)

4. The *Hydneae* have fructifications with spinous projections over which the hymenium extends. In the simpler forms the fructifications have the appearance of incrustations, with spinous outgrowths projecting from the upper surface; in other cases they have a stalk termed the STIPE, bearing an umbrella-like expansion, the PILEUS, from the under side of which the outgrowths depend. The latter form is exhibited by the edible Fungi *Hydnum imbricatum*, which has a pileus 15 cm. wide, and *Hydnum repandum* (Fig. 298), with a yellowish flesh-coloured pileus.

FIG. 298.—*Hydnum repandum*. (Reduced.)

5. In the *Polyporeae* the stalked or sessile and bracket-shaped fructifications are indented on the under side with pit-like depressions, or deep winding passages, or covered with a layer of tubes, closely fitted together and lined by the hymenium. To this family belongs the genus *Boletus*, which has a large, thick-stalked pileus, covered on the under side with a layer of narrow dependent tubes. Although many species of this genus are edible (*e.g. B. edulis*), others are exceedingly poisonous, in particular *B. Satanas* (Fig. 301). This latter Fungus has a yellow to reddish-purple stalk, with red reticulate markings above, while the pileus, which may be 20 cm. wide, is yellowish-brown on its upper surface, but on the under side is at first

blood-red, becoming later orange-red. Of the numerous species of the genus *Polyporus*, *P. fomentarius*, Touch-wood, is officinal. Its mycelium is parasitic in deciduous trees, especially the Beech, and produces large, bracket or hoof-shaped perennial fructifications, 30 cm. wide and 15 cm. thick. They have a hard, gray external surface, but inside are composed of softer, more loosely woven hyphæ, and were formerly used for tinder. The narrow tubes of the hymenium are disposed on the under side of the fructifications in successive annual layers. *P. igniarius* (Fig. 299), which is often found on Willows, and has a similar structure, has a rusty-brown colour, and furnishes, as it is much harder, a poorer quality of tinder.

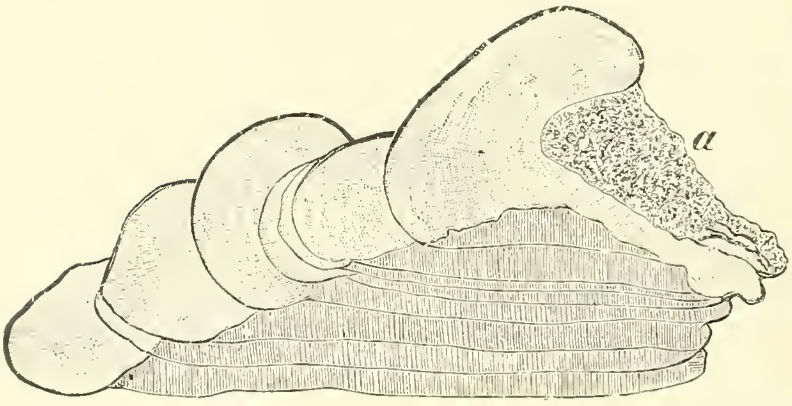


Fig. 299.—*Polyporus igniarius*. Section through an old fructification, showing annual zones of growth; *a*, point of attachment. ($\frac{1}{2}$ nat. size.)

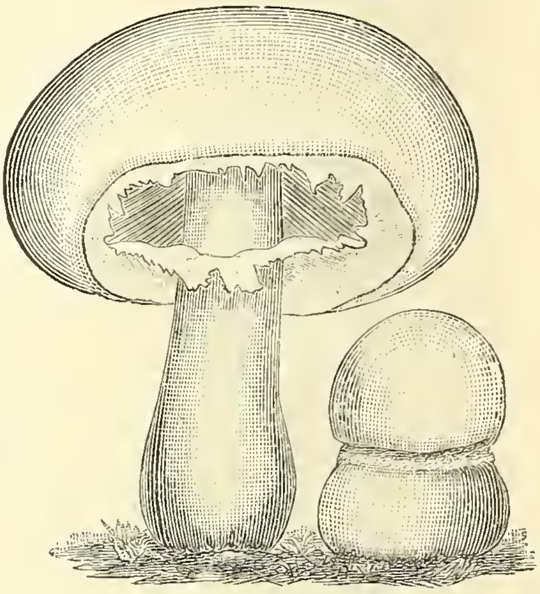


Fig. 300.—*Psalliota campestris* (= *Agaricus campestris*). To the right, a young fructification. (Reduced.)

Fig. 301.—*Boletus Satanas*. (After Krombholz, $\frac{1}{2}$ nat. size. Poisonous.)

Many parasitic *Polyporeae* are highly injurious to the trees attacked by them; thus *Heterobasidion annosum* often causes the death of whole forests of Pines and

Spruce Firs. *Merulius lacrymans* (53) is an exceedingly dangerous saprophytic species, attacking and destroying the timber of damp houses. The mycelium of this Fungus forms large, white, felted masses, giving rise to outspread, irregularly-shaped, pitted fructifications of an ochre or rusty-brown colour, and covered with a hymenial layer. Good ventilation of the infected space is the best remedial measure.

6. The *Agaricineae*, which include the greatest number of species, have stalked fructifications, commonly known as Mushrooms and Toadstools. The under side of the pileus bears a number of radially disposed lamellæ or gills which are covered with the basidia-producing hymenium. In the early stages of their formation the fructifications consist of nearly spherical masses of interwoven hyphæ, in which the stalk and pileus soon become differentiated. The rudiments of the stalk and pileus are at first enclosed in a loosely woven envelope, the VOLVA. In the course of the further development and elongation of the stalk the volva is ruptured, and its torn remnants form a ring or sheath at the base of the stalk, but in many cases its development remains rudimentary. In the "Fly Mushroom," *Amanita muscaria*, the volva is well developed, and after its rupture it is still traceable in the white scales conspicuous on the red surface of the pileus, and also on the swollen base of the stalk (Fig. 302).

FIG. 302.—*Amanita muscaria*. (½ nat. size. *POISONOUS*.)

In addition to the volva many *Agaricineae* develop a so-called VELUM, consisting of a thin membrane of hyphal tissue which extends in young fructifications from the stalk to the margin of the pileus, but is afterwards ruptured, and remains as a ring of tissue encircling the stalk (Fig. 300).

Many of the Mushrooms found growing in the woods and fields are highly esteemed as articles of food. Of edible species the following may be named: the common Field-Mushroom, now extensively cultivated, *Psalliota campestris* (Fig. 300), with whitish pileus and lamellæ at first white, then turning flesh-colour, and finally becoming chocolate-coloured; *Cantharellus cibarius*, having an orange-coloured pileus; *Lactarius deliciosus*, which has a reddish-yellow pileus, and contains a similarly coloured milky juice in special hyphal tubes; *Lepiota procera*, whose white pileus is flecked with brown scales.

Of the poisonous *Agaricineae* the following are best known: *Amanita muscaria* (Fig. 302); *Amanita bulbosa*, with whitish or yellowish pileus and the stalk swollen at the base; *Russula emetica*, with a red pileus and white lamellæ; *Lactarius torminosus*, having a shaggy yellow or reddish-brown pileus and white milky juice.

Rozites gongylophora, found in South Brazil, is of especial biological interest. According to A. MÖLLER, this species is regularly cultivated in the nests of the leaf-cutting ants. Its mycelium produces spherical swellings at the ends of the hyphæ, which become filled with protoplasm, the so-called Kohl-rabi heads, and serve the ants as food material. The ants prevent the development of the accessory conidial fructifications peculiar to this Fungus, and thus continually maintain the mycelium in their nests in its vegetative condition. The fructifications, which rarely occur on the nests, resemble those of *Amanita muscaria*, with which *Rozites* is nearly allied. According to Holtermann, the mycelium of *Agaricus rajap* is cultivated in their nests by termites in tropical Asia (54).

OFFICINAL.—*Polyporus fomentarius* (FUNGUS CHIRURGORUM). *Polyporus officinalis* (=*Boletus laricis*) gives AGARICUS ALBUS, AGARICINUM, and ACIDUM AGARICINUM.

Order 6. Gasteromycetes (45)

The *Gasteromycetes* are distinguished from the *Hymenomycetes* by their angiocarpous or enclosed fructifications, which open only after the spores are ripe, by the rupture of the outer hyphal cortex or PERIDIUM. The spores are formed within the fructifications in an inner mass of tissue termed the GLEBA; it contains numerous chambers, which are either filled with loosely interwoven hyphæ with lateral branches terminating in basidia, or whose walls are lined with a basidial hymenium.

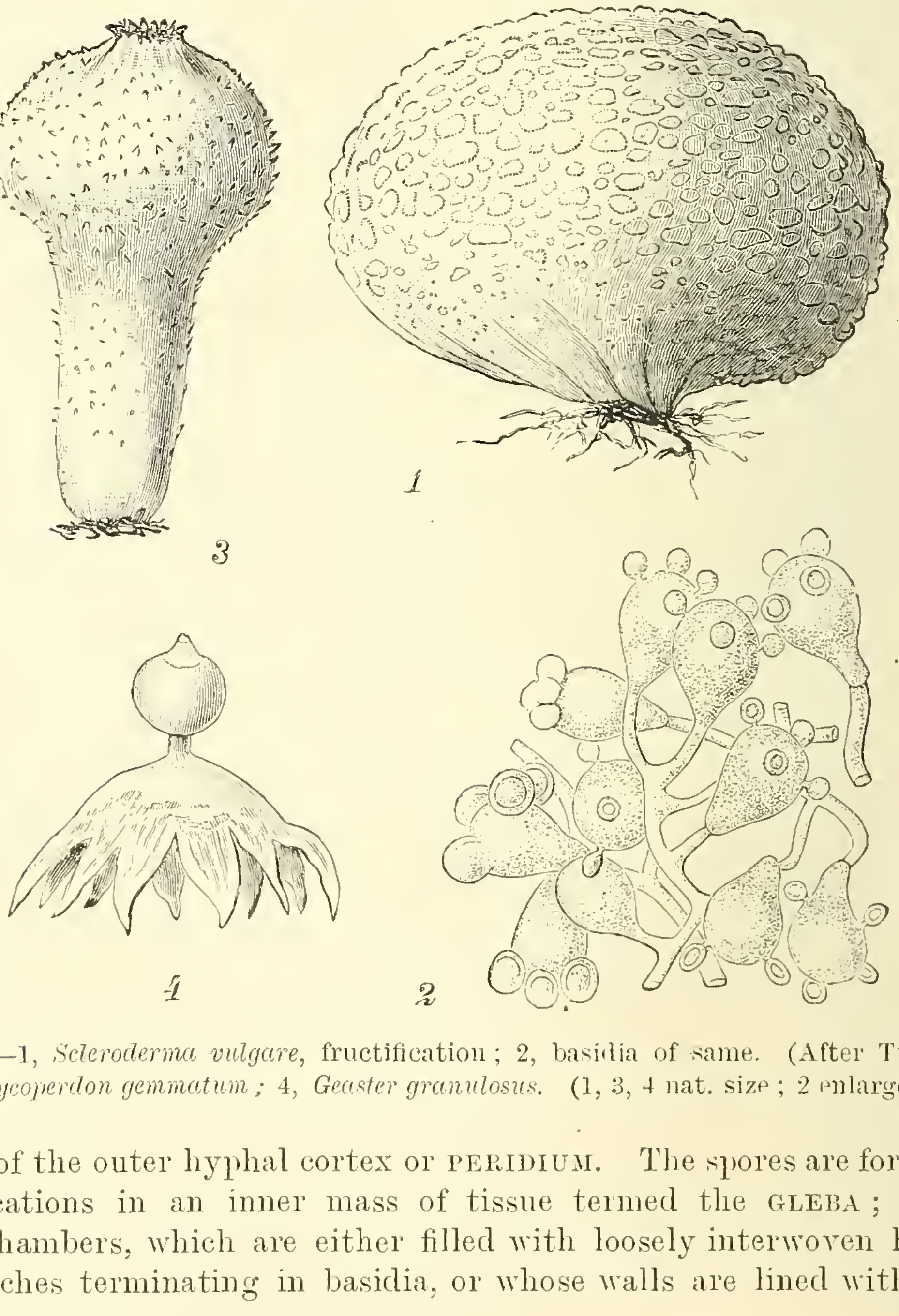


FIG. 303.—1, *Scleroderma vulgare*, fructification; 2, basidia of same. (After TULASNE.) 3, *Lycoperdon gemmatum*; 4, *Geaster granulosus*. (1, 3, 4 nat. size; 2 enlarged.)

The *Gasteromycetes* are saprophytes, and develop their mycelium in the humus soil of woods and meadows. Their fructifications, like those of the *Hymenomycetes*, are raised above the surface of the substratum, except in the group of the *Hymenogastreae*, which possesses subterranean, tuberous fructifications resembling those of the *Tuberaceae*.

The fructifications of the different genera exhibit great diversity in their structure and mode of formation.

The fructifications of *Scleroderma vulgare* (Fig. 303) have a comparatively simple structure. They are nearly spherical, usually about 5 cm. thick, and have a thick, light brown, leathery peridium which finally becomes cracked and ruptured at the apex. The gleba is black when ripe, and contains numerous chambers filled with interwoven hyphæ which produce lateral, pear-shaped basidia with four sessile spores (Fig. 303, 2). This species, which is considered poisonous, is sometimes mistaken for one of the Truffle Fungi.

The genera *Bovista* and *Lycoperdon* (Fig. 303, 3) (Puff-balls) have also spherical fructifications, which are at first white, and later of a brown colour. In the last-named genus they are also stalked, and in the case of *Lycoperdon Bovista* may even become half a metre in diameter. The peridium is formed of two layers; the outer disappears at maturity, while the inner dehisces at the summit. The hymenial layer of basidia, in the Fungi of this group, line the chambers of the gleba. The chambers are also provided with a fibrous capillitium consisting of brown, thick-walled, branched hyphæ which spring from the walls, and aid in distributing the spores. The fructifications are edible while still young and white.

In the related genus *Geaster* (Earth-star) (Fig. 303, 4) the peridia of the nearly spherical fructifications are also composed of two envelopes. When the dry fruit dehisces, the outer envelope splits into several stellate segments and the inner layer of the peridium becomes perforated by an apical opening.

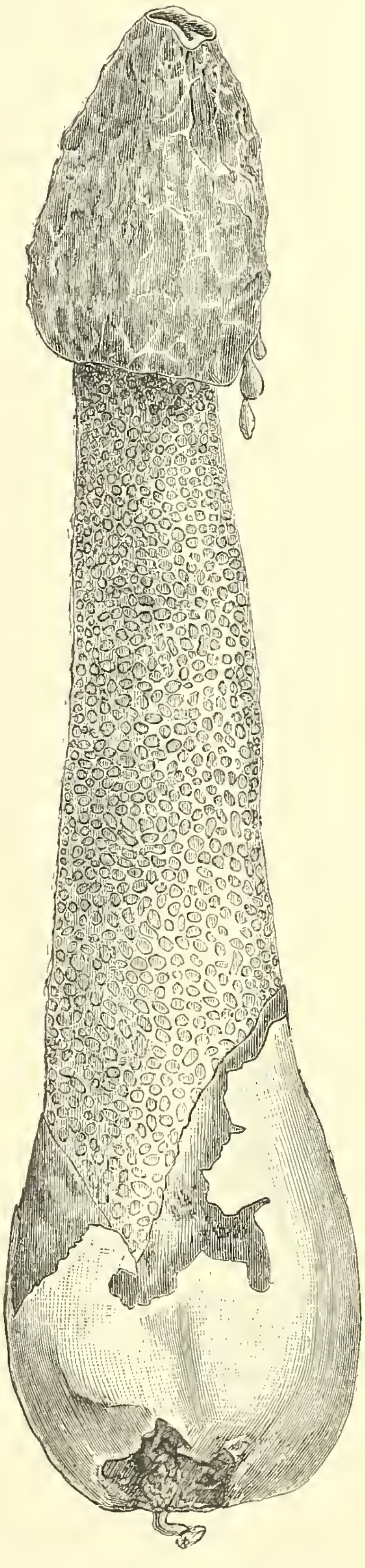


FIG. 304.—*Phallus impudicus.* (After KROMBHOLZ, ½ nat. size.)

The highest development of the fructifications is exhibited by the *Phalloideae* (55), of which *Phallus impudicus* (Stink-horn) is a well-known example. This Fungus is usually regarded as poisonous, but no poisonous effects have been proved. It was formerly employed in a salve as a remedy for gout. Its fructification recalls that of the Discomycetous *Morchella*, but it has quite a different manner of development. A fructification of this species of *Phallus* is about 15 cm. high. It has a thick, hollow stalk of a white colour and is perforated with pores or chambers. Surmounting the stalk is a bell-shaped pileus covered with a brownish-green gleba which, when ripe, is converted into a slimy mass (Fig. 304). When young the fructification forms a white, egg-shaped body, and is wholly enveloped by a double-walled peridium with an intermediate gelatinous layer. Within the PERIDIUM (also termed volva) the hyphal tissue becomes differentiated into the axial stalk and the bell-shaped pileus, carrying the gleba in the form of a mass of hyphal tissue, which contains the chambers and basidial hymenium. At maturity the stalk becomes enormously elongated, and pushing through the ruptured peridium raises the pileus with the adhering gleba high above it. The gleba then deliquesces into a dropping, slimy mass, which emits a carrion-like stench serving to attract flies, by whose agency the spores embedded in it are disseminated.

CLASS XIII

Lichenes (Lichens) ([33, 56, 58])

The Lichens are symbiotic organisms; they consist of higher Fungi, chiefly the *Ascomycetes*, more rarely *Basidiomycetes*, and unicellular or filamentous Algæ, *Schizophyceae* or *Chlorophyceae*, living in intimate connection, and together forming a compound thallus or CONSORTIUM. Strictly speaking, both Fungi and Algæ should be classified in their respective orders; but the Lichens exhibit among themselves such an agreement in their structure and mode of life, that it is more convenient to treat them as a separate class.

In the formation of the thallus the algal cells become enveloped by the mycelium of the Fungi in a felted tissue of hyphæ (Fig. 305). The Fungus derives its nourishment saprophytically from the organic matter produced by the assimilating Alga; it can send haustoria into the Algal cells, and so exhausts their contents. The Alga, on the contrary, derives a definite advantage from its consortism with the Fungus, receiving from it inorganic substances and water (cf. p. 212). From the symbiosis entered into by a Lichen Fungus with an Alga, a dual organism results with a distinctive thallus, the form of which, influenced by the mode of nutrition of the independently assimilating Alga, differs greatly from that of other non-symbiotic Hyphomycetes, and rather resembles that of Algæ and Liverworts.

In their adaptation to the requirements of the two constituent members, the thalli of the Lichens exhibit a variety of forms which, although sometimes made use of as a means of classification, are of no value in indicating natural relationships.

The simplest Lichens are the FILAMENTOUS, with a filiform branched thallus consisting of algal filaments interwoven with Fungus hyphæ. An example of such a filamentous form is presented by *Ephebe pubescens*, which is found growing on damp rocks in short, delicately branched tufts.

Another group is formed by the GELATINOUS Lichens, whose thallus, usually foliaceous, is of a gelatinous nature. The Algæ inhabiting the thalli of the gelatinous Lichens belong to the families of the *Chroococcaceae* and *Nostocaceae*. As is characteristic of the

Nostocs, their cell walls are swollen, forming a gelatinous mass traversed by the hyphæ of the fungus. The genus *Collema* is an example of this group.

In both the filamentous and gelatinous Lichens the Algæ and Fungus hyphæ are uniformly distributed through the thallus, which is then said to be unstratified or HOMOIOMEROUS.

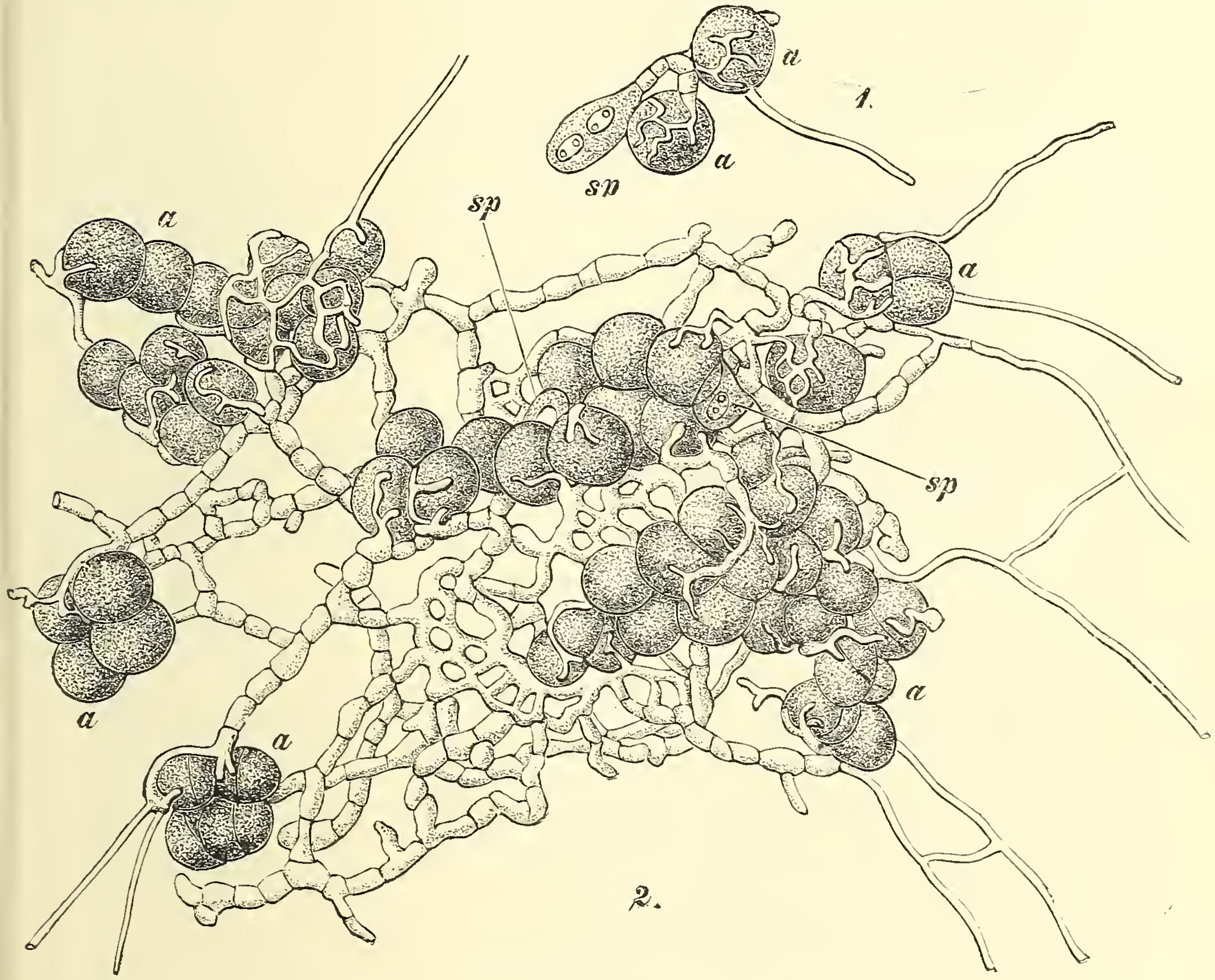


FIG. 305.—*Xanthoria parietina.* 1, Germinating ascospore (*sp*) with branching germ-tube applied to the *Cystococcus* cells (*a*); 2, thallus in process of formation, *sp*, two ascospores; *p*, *Cystococcus* cells. By the fusion of the hyphæ in the middle of the mycelium, a pseudo-parenchymatous, cortical layer has begun to form. (After BONNIER, from V. TAVEL, × 500.)

The other Lichens have stratified or HETEROMEROUS thalli. The enclosed Algæ are usually termed GONIDIA. They are arranged in a definite GONIDIAL LAYER covered, externally, by a CORTICAL LAYER, devoid of algal cells and consisting of a pseudo-parenchyma of closely-woven hyphæ. It is customary to distinguish the three following forms of heteromerous Lichens.

1. CRUSTACEOUS LICHENS, in which the thallus has the form of an incrustation adhering closely to a substratum of rocks or to the soil, which the hyphæ to a certain extent penetrate.

2. FOLIACEOUS LICHENS (Fig. 306), whose flattened, leaf-like lobed or deeply-cleft thallus is attached more loosely to the substratum by

means of rhizoid-like hyphæ (rhizines), springing either from the middle only or irregularly from the whole under surface.

3. FRUTICOSE LICHENS (Fig. 307), with a filamentous or band-like thallus branched in a shrub-like manner and attached only at the base. They are either erect or pendulous, or may sometimes lie on the surface of the substratum.

In their natural condition the germinating spores of the Lichen Fungi appear to be capable of continuing their further development only when they are enabled to enter into symbiosis with the proper gonidia. For a few genera of Lichens, however, it has been determined that the Fungi sometimes exist in nature without the presence of the Algæ; it has been shown that the tropical Lichen, *Cora pavonia* (Fig. 313), whose Fungus belongs to the order *Hymenomycetes*, may produce fructifications even when deprived of its Alga, which have a form resembling those of the Fungus genus *Thelephora*. Small thalli have also been successfully grown from the spores of certain Lichen-forming Ascomycetes, cultivated without Algæ and supplied with a proper nutrient solution.

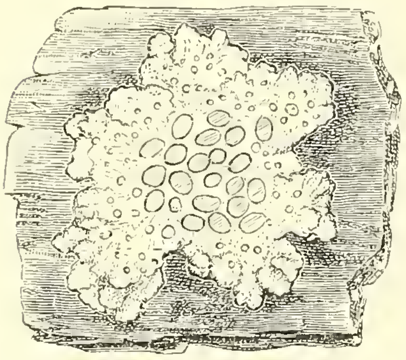


FIG. 306.—*Xanthoria parietina* on a piece of bark. (Nat. size.)

Many Lichens are able to multiply in a purely vegetative manner, by means of loosened pieces of the thallus, which continue their growth and attach themselves to the substratum with new rhizines. The majority of the heteromerous Lichens possess in the gonidial layer another means of vegetative multiplication by forming SOREDIA. In this process, small groups of dividing gonidia become closely entwined with mycelial hyphæ, and form small isolated bodies which, on the rupture of the thallus, are scattered in great numbers by the wind and give rise to new Lichens.

The fructifications of the Lichens are produced by the consorting Fungi, not by the vegetating Algæ. The Fungi belong in nearly every case to the *Ascomycetes*, in only a single genus to the *Hymenomycetes*.

1. Ascolichenes

Only a few genera of Lichens have flask-shaped perithecia, the Fungus belonging to the *Pyrenomycetes* (*Endocarpon*, *Verrucaria*). Most genera produce, as the ascus-fruit of their Fungus, cupular or discoid apothecia, sessile or somewhat depressed on the thallus. In structure they resemble those of the *Pezizeae* (Fig. 280), and bear on their upper side an hymenium of asci and paraphyses. One of the commonest species of fruticose Lichens belonging to this group is *Usnea barbata*, the Beard Lichen, frequently occurring on trees and having large, fringed apothecia (Fig. 307). *Roccella tinctoria*, found widely distributed on the rocks of the African coast and East Indies, has an erect, vermiform, forked thallus from which litmus and orchil (orseille) are obtained. *Cetraria islandica*, Iceland Moss (Fig. 308), occupies an intermediate position between the fruticose and foliaceous Lichens. It has a divided, foliaceous but partially erect thallus, which is of a light bluish green or brown colour, whitish on the under side, and bears the apothecia obliquely on its margin. This Lichen is found in mountainous regions in the northern part of the Northern Hemisphere, and also at Cape Horn; it has an officinal value as a demulcent. *Xanthoria parietina* (Fig. 306) may be taken as an example of one of the commonest of the foliaceous Lichens. The thallus is orange-yellow in colour, and bears numerous apothecia on its central portions. *Graphis scripta* may be cited as a well-known example of the crustaceous Lichens; its grayish white thallus occurs on the bark of trees, particularly of the Beech, on whose surface the apothecia are disposed as narrow, black furrows resembling writing. To the crustaceous Lichens belongs also *Sphaerothallia esculenta*, growing on rocks in the steppes and deserts of North Africa and Asia. The thallus falls into small pieces the size of a pea; scattered by the wind they are utilised by the Tartars in the preparation of earth-bread.

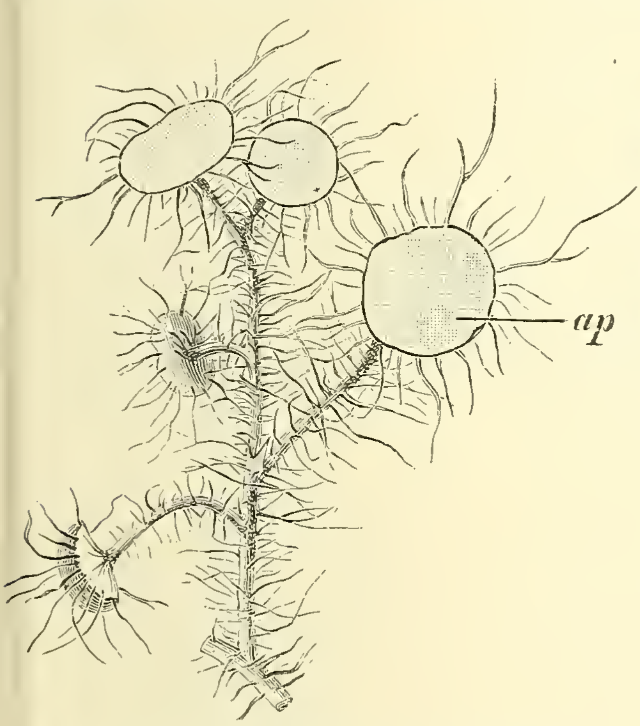


FIG. 307.—*Usnea barbata.* *ap*, Apothecium. (Nat. size.)

FIG. 308.—*Cetraria islandica.* *ap*, Apothecium. (Nat. size. OFFICINAL.)

A peculiar mode of development is exhibited by the genus *Cladonia* (57), whose primary thallus consists of small horizontal scales attached directly to the ground, from which rises an erect portion, the PODETIUM, of varying form and structure in the different species. In some cases the podetia are stalked and funnel-shaped, bearing on the margin or on outgrowths from it knob-like apothecia, which in *C. pyxidata* are brown, in *C. coccifera* (Fig. 309) bright red. In other species the erect podetia are slender and cylindrical, simple or forked; in *C. rangiferina*, Reindeer Moss, which has a world-wide distribution, particularly in the tundras of the North, the podetia are finely branched (Fig. 310), and bear the small brown apothecia at the ends of the branches. Frequently the podetia of this species and often also of the others remain sterile,

FIG. 309.—*Cladonia coccifera.* *t*, Scales of primary thallus. (Nat. size.)

and the ascogenous hyphæ, although differentiated in the interior, do not succeed in producing asci.

The ascus-fructifications (apothecia or perithecia) of the Lichens originate, as Stahl (58) was the first to prove, from carpogonia which are frequently present in large numbers on young lobes of the thallus. The carpogonium (Fig. 311) is here a multicellular filament, the lower part of which is spirally coiled, while it continues above into a trichogyne composed of elongated cells, and projecting from the surface of the thallus. All the cells are uninucleate and communicate with one another by means of pits. Those of the lower part of the filament contain abundant protoplasm. Apart from their multicellular nature these structures recall the carpogonia found in the *Florideae*. The spermatia, which originate in spermogonia, are presumably the male sexual cells. The spermatia are round or rod-shaped cells abstricted from the ends of hyphæ, which line the spermogonium

Fig. 310.—*Cladonia rangiferina*. *A*, Sterile; *B*, with ascus-fruit at the ends of the branches. (Nat. size.)

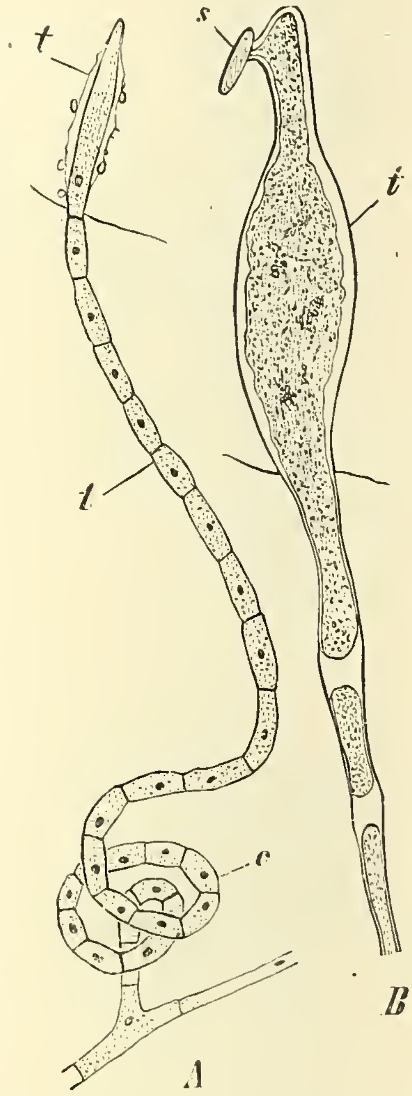


Fig. 311.—*Collema crispum*. *A*, Carpogonium (*c*) with its trichogyne (*t*). (× 405.) *B*, Apex of the trichogyne with the spermatium (*s*) attached (× 1125.) (After E. Baur.)

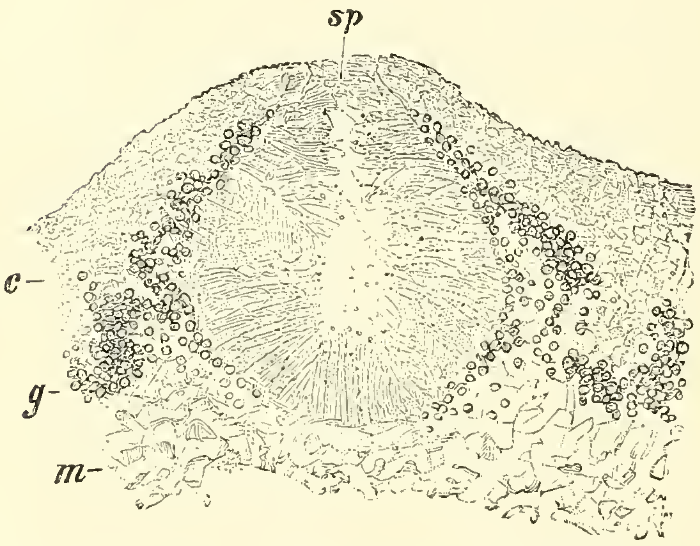


Fig. 312.—Section through a spermogonium (*sp*) in the thallus of *Anaptychia ciliaris*; *c*, cortical layer; *m*, medullary layer; *g*, gonidial layer. (× 90.)

(Fig. 312); after their liberation they conjugate with the adhesive tip of the trichogyne (Fig. 311, *B*). After conjugation the spermatia appear empty and their nucleus has disappeared. When this has taken place the cells of the trichogyne collapse, while the cells of the coiled carpogonium swell, undergo divisions, and form the ascogonium. From the latter the ascogenous hyphæ which bear the asci are produced. The vegetative hyphæ composing the fructification and the paraphyses originate from hyphæ which arise below the carpogonium. The fructification may arise from one or from several carpogonia. The behaviour of the sexual nuclei requires further investigation. When the sexual organs of Lichens are compared with those of the *Ascomycetes*, it is noteworthy that tubular antheridia (such as those of the *Erysipheae* and *Pyronema*) have not been observed in the former group. The male sexual cells of Lichens have an entirely different origin, and are more readily compared with the spermatia of the *Florideae*. The spermogonia and spermatia further correspond closely in their structure with the pycnidia and pycnospores of the *Ascomycetes* and the *Uredineae*. It has even been shown by A. MÖLLER that the spermatia of Lichens can germinate and produce a mycelium. On this account BREFELD and MÖLLER regard the spermatia as conidia and dispute the sexuality of the Lichens.

2. Hymenolichenes (59)

The *Hymenolichenes* are represented only by the tropical *Cora pavonia*, of which the genera *Dictyonema* and *Laudatea* are only specially differentiated forms. The Fungus of this Lichen belongs to the family *Thelephoreae* (p. 365); its flat, lobed, and often imbricated fructifications are also found entirely devoid of Algæ. In symbiosis with the unicellular Alga *Chroococcus*, it forms the fructifications of *Cora pavonia* (Fig. 313), resembling those of the Thelephoras with a channelled, basidial hymenium on the under side. Associated symbiotically, on the other hand, with filaments of the blue-green Alga *Scytonema*, if the Fungus preponderates, it produces the bracket-like Lichens of the *Dictyonema* form, found projecting from the limbs of trees with a semicircular or nearly spherical thallus composed of radiating hyphal threads, and having the hymenium on the under side. When the shape of the thallus is determined by the Alga, a Lichen of the *Laudatea* form occurs as felted patches of fine filaments on the bark of trees, with the hymenium on the parts of the thallus which are turned away from the light.

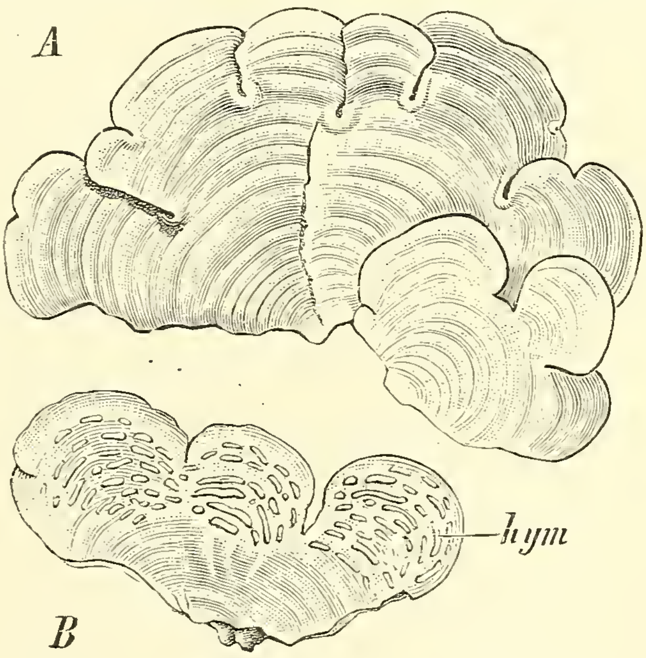


FIG. 313.—*Cora pavonia*. *A*, Viewed from above; *B*, from below; *hym*, hymenium. (Nat. size.)

OFFICINAL.—The only representative of the Lichens is *Cetraria islandica* (LICHEN ISLANDICUS).

II. BRYOPHYTA (MOSSES) (60, 61)

The Bryophyta or Muscineae comprise two classes, the *Hepaticae* or Liverworts, and the *Musci* or Mosses. They are distinguished from the Thallophyta by the characteristic structure of their sexual organs, ANTHERIDIA and ARCHEGONIA, which are similar to those of the Pteridophyta, the most highly developed of the Cryptogams. The Bryophyta and Pteridophyta are accordingly regarded as having been derived from a common ancestor, and, in contrast to the Thallophyta, they are referred to collectively as *Archegoniatae*.

The ANTHERIDIA or male sexual organs are stalked, ellipsoidal, spherical, or club-shaped, with thin walls formed of one layer of cells and enclosing numerous small cells, each one of which is the mother cell of a spermatozoid (Fig. 314). At maturity the spermatozoid mother cells separate and are ejected from the antheridium, which ruptures at the apex. By the eventual dissolution of the enveloping walls of the mother cells the spermatozoids are set free as short, slightly twisted filaments, terminating anteriorly in two long cilia.

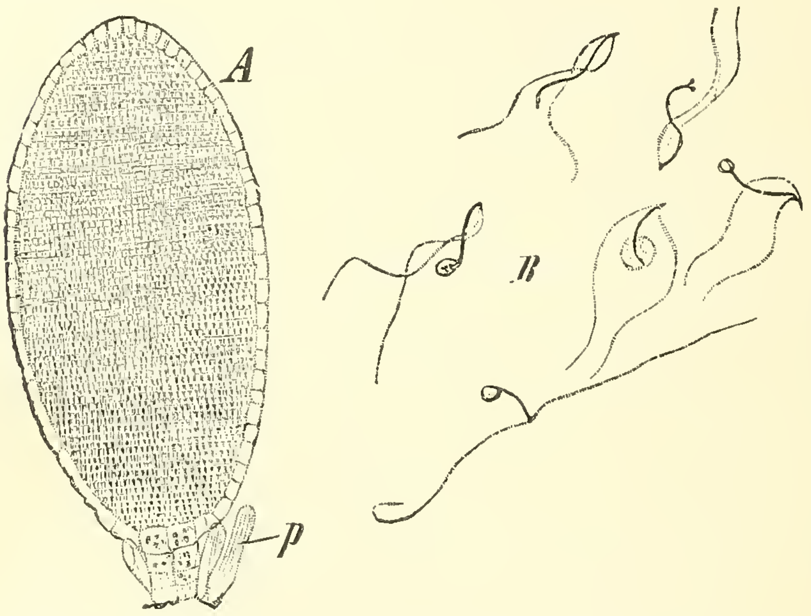


FIG. 314.—*Marchantia polymorpha.* *A*, Nearly ripe antheridium in optical section; *p*, paraphyses. *B*, Spermatozoids fixed with 1 per cent perosmic acid. (*A* × 90, *B* × 600.)

The ARCHEGONIA are flask-shaped bodies with walls formed of but one layer of cells; they are sessile or shortly stalked, sometimes also somewhat sunk in the tissue, and consist of a dilated ventral portion and a long, slender neck. The ventral portion encloses a large central cell, the contents of which shortly before maturity divide into the egg-cell (Fig. 315, *A*, *o*) and into an overlying ventral canal-cell (*k''*). The latter is situated at the base of the neck, just below a central row of neck-canal-cells (*k'*). On the maturity of the archegonium, the ventral and neck-canal-cells become mucilaginous and disorganised. If water is present, the cells at the apex of the neck separate (*E*) and the mucilaginous matter is discharged, and exerts through the diffusion of certain of its constituents in the water (cane-sugar in the case of Mosses) an attractive stimulus on the spermatozoids. The spermatozoids, thus directed toward the neck of the archegonium, traverse it as far as the egg, into which one spermatozoid penetrates. The water necessary for the process of fertilisation is sufficiently supplied by rain or dew. After fertilisation has been accomplished, the egg-cell divides and gives rise directly to an embryo (*C*), without first, as is usually the case in the oogamous Thallophyta, undergoing a period of rest.

The Mosses as well as the Pteridophytes multiply also asexually by means of walled SPORES adapted for dissemination through the air. These two modes of reproduction, sexual and asexual, occur in regular alternation, and are confined each to a sharply distinct generation; a sexual, provided with sexual organs, and an asexual, which produces spores. The sexual generation arises from the spore; the asexual from the fertilised egg. THIS ALTERNATION OF GENERATIONS is characteristic of all Archegoniatae.

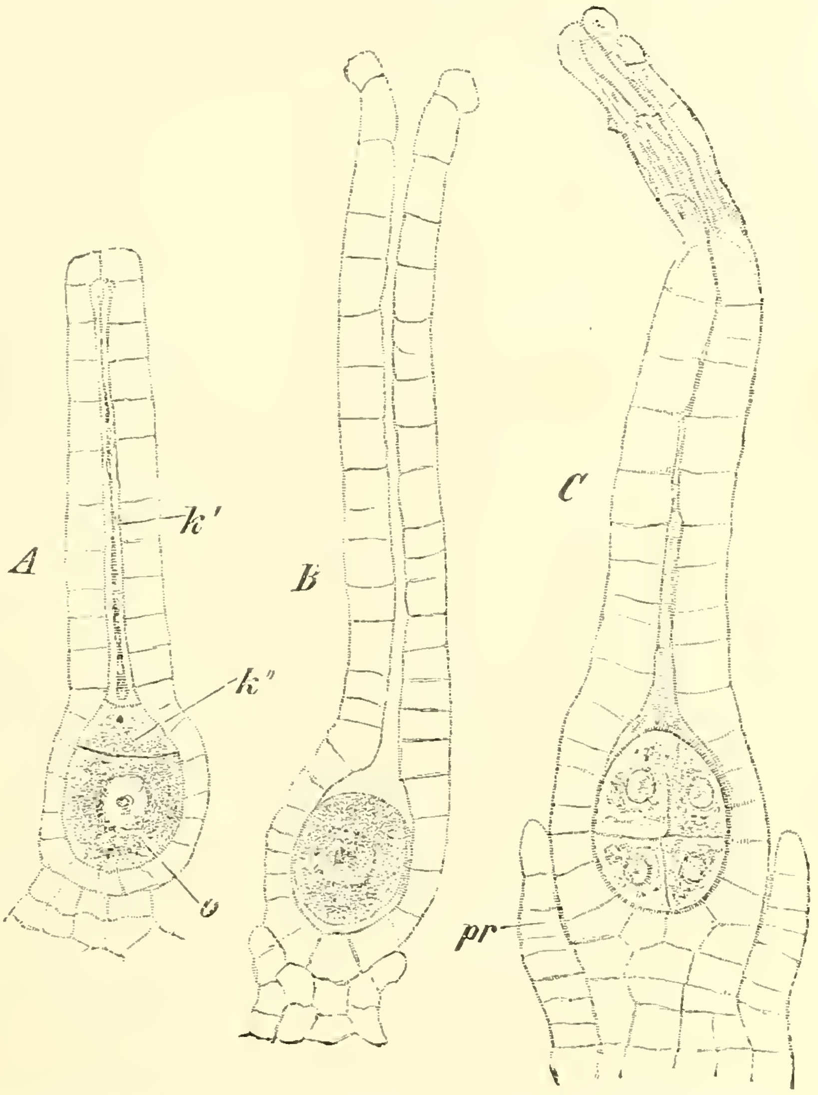


FIG. 315.—*Marchantia polymorpha*. *A*, Young, *B*, mature archegonium; *C*, fertilised archegonium, with dividing egg-cell; *k'*, neck-canal-cell; *k''*, ventral canal-cell; *o*, egg-cell; *pr*, pseudo-perianth. (× 540.)

In the development of the SEXUAL GENERATION, the unicellular spore on germinating ruptures its outer coat or EXINE, and gives rise to a germ-tube. In the case of the *Hepaticae*, the formation of the plant at once commences, but in most of the *Musci* a PROTONEMA is first produced, which resembles in structure the filaments of confervoid Algæ, and is composed of cells containing chlorophyll (Fig. 316, *A*, *B*). The green, filamentous protonema gives rise to branched, colourless rhizoids (*r*), which penetrate the substratum. The MOSS-PLANTS arise from buds developed on the protonema at the base of the branches. Protonema and Moss-plant together represent the sexual generation. Many Liverworts possess a thallus consisting of dichotomously branching lobes, which is attached to the substratum at its base or on the under side by means of rhizoids, thus repeating the vegetative structure of many Algæ (cf. Fig. 8 with Fig. 10). In other *Hepaticae*, on the other hand, and in all the *Musci*, there exists a distinct differentiation into stem and leaves (Fig. 329). In no instance, however, are true roots formed consisting of a tissue of cells, but in their stead rhizoids, consisting of colourless branching filaments. The Bryophytes, in this respect, differ essentially from the Pteridophytes, which are provided with true roots. The stems and leaves of Mosses are also anatomically of a simple structure; if conducting strands are present, they are composed merely of simple elongated cells. The sexual organs are produced on the adult, sexual generation; in the thalloid forms, on the dorsal side of the thallus; in the cormophytic forms, at the apex of the stem or its branches (Fig. 317).

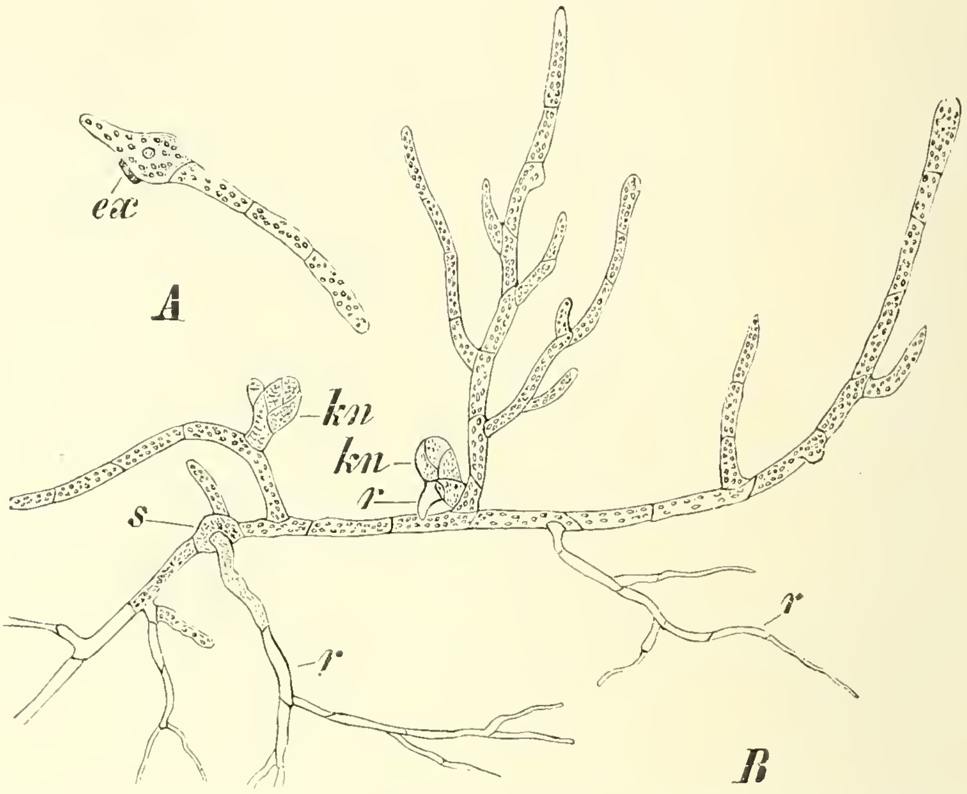


FIG. 316.—*Funaria hygrometrica.* *A*, Germinating spore; *ex*, exine; *B*, protonema; *kn*, buds; *r*, rhizoids; *s*, spore. (After MÜLLER-THURGAU; magnified.)

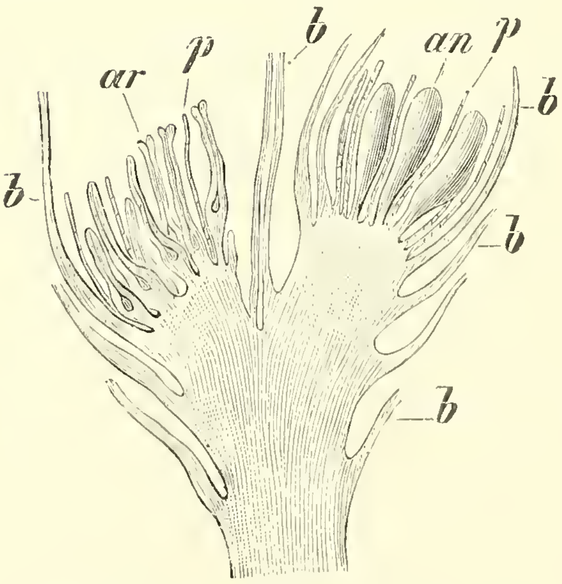


FIG. 317.—*Phascum cuspidatum.* *an*, Antheridia; *ar*, archegonia at the apex of the bifurcated moss stem; *b*, leaves; *p*, paraphyses. (After HOFMEISTER, × 45.)

By the division of the fertilised egg, a multicellular embryo is formed, which, by its further development, gives rise to the second or ASEXUAL GENERATION, represented by the SPOROGONIUM or the stalked MOSS CAPSULE. The sporogonium, in most cases, consists of a round or oval capsular receptacle, in whose internal tissue numerous unicellular spores are produced. At maturity the capsule opens and sets free the spores. In both the Bryophytes and Pteridophytes the spores are formed in TETRADS by the twice-repeated division of the spore-mother-cells, which previously become disunited, and represent the actual point of commencement of the sexual generation. The spore capsule has usually a shorter or longer stalk, of which the basal portion, or foot, remains in the distended venter of the archegonium, and, in consequence of the overgrowth of the underlying tissue, has the appearance of being sunk in it. Although the sporogonium constitutes a distinct asexual generation, it continues throughout its existence united with the sexual generation, and draws from it the nourishment necessary for its development.

The two classes comprising the Bryophytes may be briefly characterised as follows :—

1. *Hepaticae* (Liverworts).—The sexual generation, with poorly developed and generally not distinctly differentiated protonema, has either a dichotomously divided thallus or is developed as a leafy, and, with few exceptions, dorsiventral shoot. In the majority of *Hepaticae*, in addition to spores, the capsule produces also elaters, sterile cells which, in their typical development, become greatly elongated and provided with spiral thickenings (Fig. 321, *F*). They conduct nourishment to the developing sporogenous cells, and at maturity, after the opening of the capsule, serve to separate and scatter the spores. Only in one order, *Anthocerotaceae*, does the capsule have a columella, or an axial mass of sterile cells, which also conduct the metabolic products to the developing spores.

2. *Musci* (Mosses).—The protonema of the sexual generation is usually well developed and distinctly defined, and the moss plant is always segmented into stem and leaves. The leaves are arranged spirally in polysymmetrical, less frequently in bisymmetrical, rows. The capsule is always without elaters, but, except in one genus, it always possesses a columella.

CLASS I

Hepaticae (Liverworts) (62)

The Hepaticae are divided, according to the structure of the sporogonium and the segmentation exhibited by the sexual generation, into four orders: the *Ricciaceae*, *Marchantiaceae*, and *Anthocerotaceae*, comprising exclusively thalloid forms; and the *Jungermanniaceae*, including both thalloid and foliose forms.

Order 1. Ricciaceae

Of all the *Hepaticae*, this order has the simplest structure. The genus *Riccia* belongs to this order ; its dichotomously-lobed or cleft thallus forms small rosettes, and grows on damp or marshy soil (Fig. 318, *A*). *Riccia natans* is found floating, like Duckweed, on the surface of stagnant water. *Riccia fluitans*, on the other hand, lives wholly submerged, and has narrow, more profusely branching, thalloid segments (Fig. 10); it can, however, grow on marshy soil, and then forms flat rosettes. The Riccias are provided with fine rhizoids springing from the under side of the thallus (Fig. 318, *B*), and possess, in addition, a double row of transversely disposed ventral scales, consisting of a single layer of cells, which also function in the absorption of nourishment. Both organs are wanting in the submerged species, *Riccia fluitans*, which may accordingly be regarded as representing the simplest form of Liverworts.

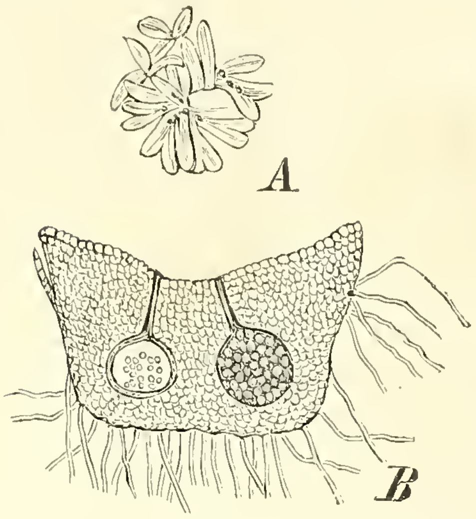


FIG. 318.—*Riccia minima*. *A*, Thallus with sporogonia sunk in the tissue at the base of the lobes (nat. size); *B*, slightly magnified section through a thallus lobe. (After BISCHOFF.)

The antheridia and archegonia are sunk in the surface of the upper side of the thallus. From the fertilised egg-cell is developed a spherical sporogonium, filled with large tetrahedral spores. The wall of the sporogonium consists of a single layer of cells; it becomes disorganised during the ripening of the spores, which are eventually set free by the rupture and disintegration of the venter and the surrounding cells of the thallus.

Order 2. Marchantiaceae

The Liverworts included in this order are much more highly organised, and in many genera they have a decidedly complicated structure. *Marchantia polymorpha*, found growing on damp soil, may serve as an example. It forms a flat, deeply-lobed, dichotomously-branched thallus, about two centimetres wide, and having an inconspicuous midrib (Fig. 320, *A*; Fig. 321, *A*). From the under side of the thallus spring unicellular rhizoids, of which some have smooth walls, others conical thickenings projecting into the inner cavity. The thallus is provided also with ventral scales, consisting of a single layer of cells. In its internal development a dorsiventral structure is also apparent. With the naked eye it may be seen that the upper surface of the thallus is divided into small rhombic areas. Each area is perforated by a central air-pore leading into a corresponding air-chamber immediately below (Fig. 159, *A*, *B*). The lateral walls of the air-chambers determine the configuration of the rhombic areas. The air-pore in the roofing wall of each chamber is in the form of a short canal, bounded by a wall formed of several tiers of cells, each tier comprising four cells. Numerous short filaments, consisting of rows of nearly spherical cells containing chlorophyll grains, project from the floor of the air-chambers and perform the functions of assimilating tissue. Chlorophyll grains are found also in the walls of the chambers, but only in small numbers. The air-chambers merely represent depressions in the outer surface which have become roofed over by the more rapid growth of the adjacent epidermal cells. The intensity of the illumination exercises a great influence on the formation of the air-chambers; when the illumination is very weak they may not occur at all. The epidermis on the under side of the thallus is formed of one layer of cells. The tissue below the air-chamber layer is devoid of chlorophyll, and consists of large parenchymatous cells, which function as accumulatory or reservoir cells.

Small cup-shaped outgrowths with toothed margins, the gemmiferous receptacles or cupules, are generally found situated on the midribs on the upper surface of the thallus (Fig. 320, *b*). These contain a number of stalked gemmæ, flat, biscuit-shaped bodies of a green colour. The gemmæ arise by the protrusion and repeated division of a single epidermal cell (Fig. 319); at maturity they become detached from the stalk (at *x*, Fig. 319, *D*). They are provided with two growing points, one at each of the marginal constrictions, from which their further development into new plants proceeds. On cross-section (*E*) they are seen to be composed of several layers of cells; some of the cells are filled with oil globules (*D*, *o*), while from other colourless cells rhizoids develop. Cells containing oil are also present in the mature thallus, and are of frequent occurrence in all the *Hepaticae*. By means of the abundantly developed gemmæ *Marchantia* is enabled to multiply vegetatively to an enormous extent.

The sexual organs, antheridia and archegonia, are borne on special erect branches of the thallus. The reproductive branches, which are rolled together at the lower end into a stalk, expand above into a profusely-branched upper portion. In this species, which is diœcious, the antheridia and archegonia develop on different plants. The branches producing the male organs terminate in lobed discs, which bear the antheridia on their upper sides in flask-shaped depressions, each containing an antheridium (Fig. 320, *B*). The depressions, into each of which a narrow canal leads, are separated from each other by tissue filled with air-chambers. (The structure of the antheridia and spermatozoids is illustrated by Fig. 314 and the accompanying description.)

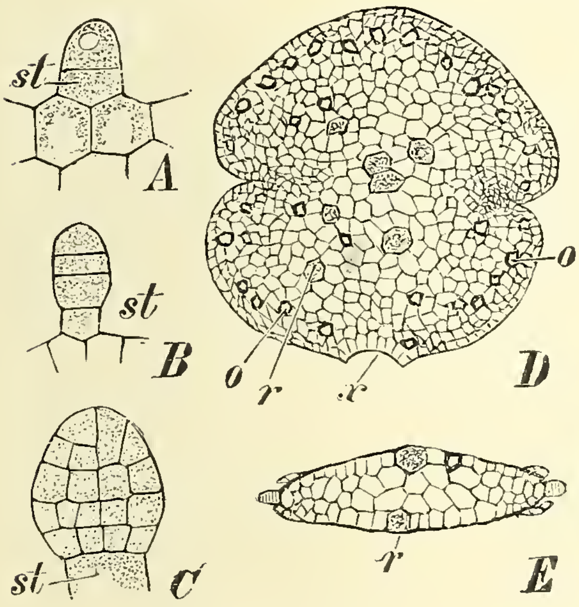


FIG. 319.—*Marchantia polymorpha*. *A*-*C*, Successive stages in the formation of a gemma; *st*, stalk-cell; *D*, surface view; *E*, transverse section of a gemma; *x*, point of attachment to stalk; *o*, oil cells; *r*, colourless cells with granular contents, from which the rhizoids will develop. (After KNY, *A*-*C* × 275; *D*-*E* × 65.)

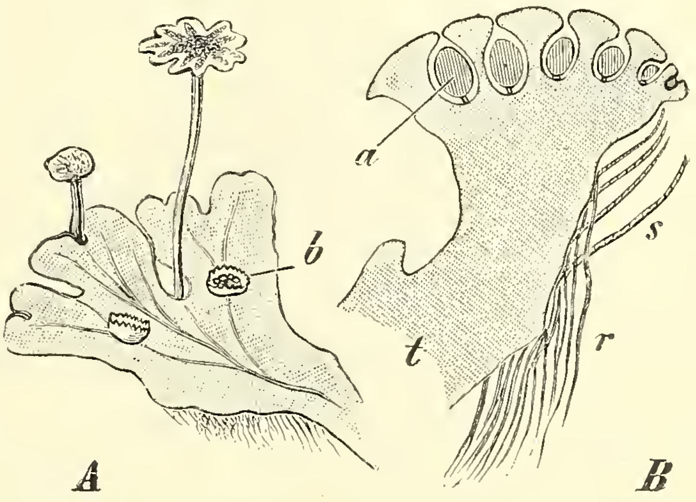


FIG. 320.—*Marchantia polymorpha*. *A*, A male plant, with antheridiophores and cupules *b* (nat. size); *B*, section of young antheridiophore; *a*, antheridia; *t*, thallus; *s*, ventral scales; *r*, rhizoids. (Somewhat magnified.)

The female branches terminate each in a nine-rayed disc (Fig. 321, *A*). The upper side of the disc, between the rays, is turned underneath in the process of growth, and, as the archegonia are borne on these portions, they seem to arise from the under side. The archegonia are disposed in radial rows between the rays, each row being enveloped in a toothed lamella or sheath (Fig. 321, *B*, *C*, *h*; for structure of the archegonia see Fig. 315, and description).

The fertilised egg-cell gives rise to a multicellular embryo (Fig. 315, *C*), and this, by further division and progressive differentiation, develops into a stalked oval sporogonium. The capsule of the sporogonium is provided with a wall consisting of one layer of cells, and ruptures at the apex to let free the spherical spores.

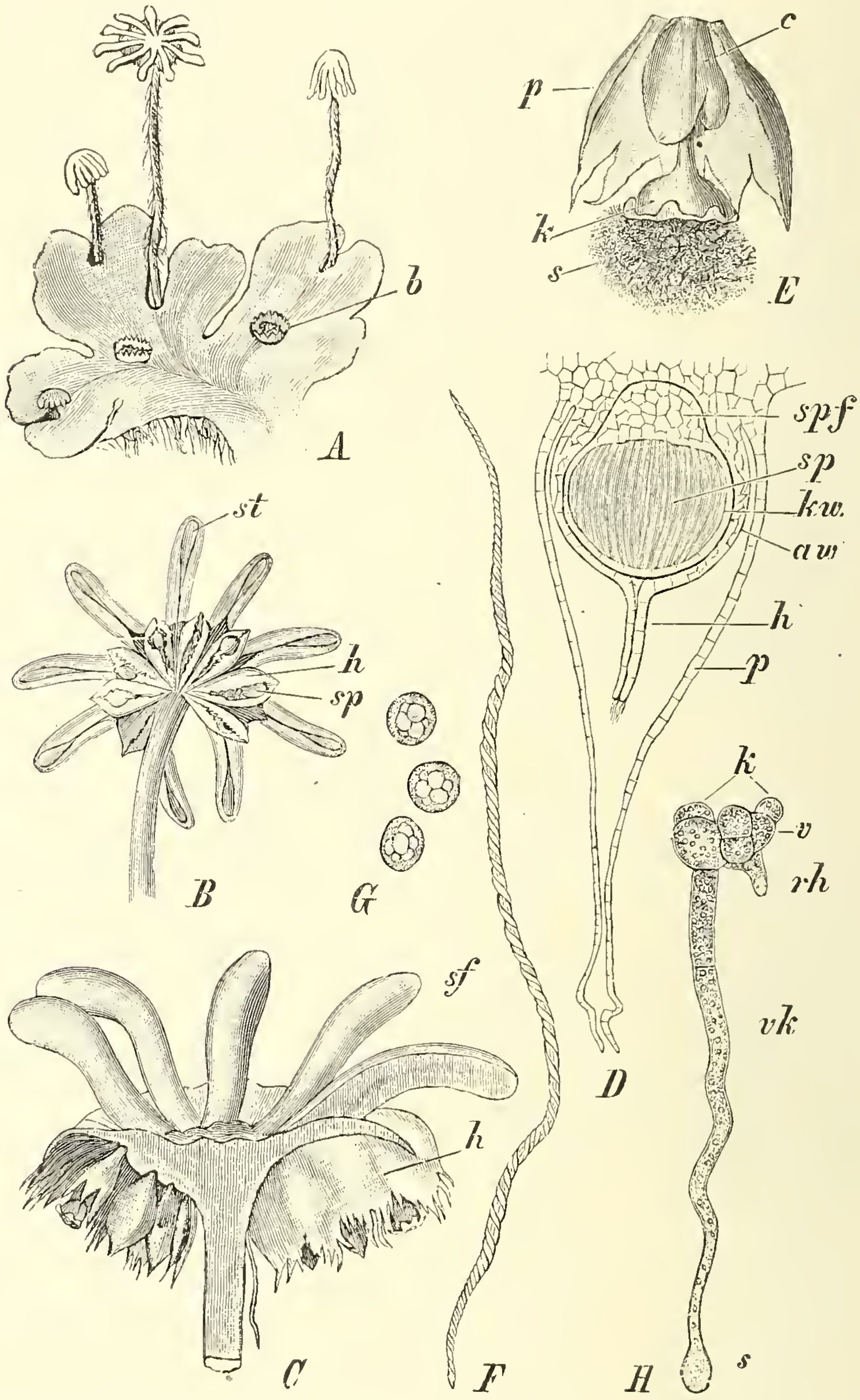


Fig. 321.—*Marchantia polymorpha.* *A*, A female plant, with four archegoniophores of different ages ; *b*, cupules (nat. size) ; *B*, under side of receptacle ; *st*, rays ; *h*, sheath ; *sp*, a sporogonium (× 3) ; *C*, half of a receptacle, divided longitudinally (× 5) ; *D*, longitudinal section of a young sporogonium ; *spf*, the foot ; *sp*, sporogenous tissue ; *kw*, wall of capsule ; *aw*, wall, and *h* neck, of archegonium ; *p*, pseudo-perianth (× 70) ; *E*, ruptured sporogonium ; *k*, capsule ; *s*, spores and elaters ; *p*, pseudo-perianth ; *c*, archegonial wall (× 10) ; *F*, an elater ; *G*, ripe spores (× 315) ; *H*, germinating spore (*s*) ; *vk*, protonema ; *k*, germ-disc, with the apical cell *v* and rhizoid *rh* (× 100). (*C*, *E* after Bischoff ; *B*, *D*, *F-H* after Kny.)

The elaters, or elongated, spirally thickened, fibre-cells formed in the capsules, between the spores, by the prolongation of definite cells, are characteristic of the Marchantias and most of the Liverworts. The elaters are discharged from the ruptured capsule, together with the spores, and serve for their dispersion in the same way as the capillitium of the *Myxomycetes* (Fig. 321, *E, F, G*). The ripe capsule, before the elongation of the stalk, remains enclosed in the archegonium wall (*D, aw*), which, for a time, keeps pace in its growth with that of the capsule. As the stalk elongates, the archegonium wall or calyptra is broken through and remains behind, as a sheath, at the base of the sporogonium (*E, c*). The capsule is surrounded also by the pseudo-perianth, an open sac-like envelope which grows, before fertilisation, out of the short stalk of the archegonium (Fig. 315, *C, pr;* Fig. 321, *D, E, p*). Similar envelopes occur in the higher *Hepaticae*, in which they constitute a true perianth, and arc formed of leaves.

Marchantia was formerly used in the treatment of diseases of the liver; this fact explains the origin of the name Liverwort.

Order 3. Anthocerotaceae

The few forms included in this order have an irregular, disc-shaped thallus, which is firmly anchored to the soil by means of rhizoids. The cells of the thallus contain, in contrast to those of other Bryophyta, a single large chloroplast. The antheridia arise, in groups of two to four, by the division of a cell lying below the epidermis; they remain enclosed in cavities in the upper side of the thallus until maturity. The archegonia are at first merely sunk in the upper surface of the thallus, but after fertilisation they become covered over by a many-layered wall formed by the overarching growth of the adjoining tissue. This enveloping wall is afterwards ruptured by the elongating capsule, and forms a sheath at its base. The sporogonium consists of a swollen foot and a long, pod-shaped capsule; it has no stalk. The capsule splits longitudinally into two valves, and has a central hair-like columella formed of a few rows of sterile cells (Fig. 322). The columella does not extend to the apex of the capsule, but is surmounted by a narrow layer of sporogenous cells. Elaters also occur; they are multicellular, variously shaped, and often forked. The sporogonia, unlike those of all other *Hepaticae*, do not ripen simultaneously throughout their whole length, but from the tips downwards, and continue to elongate by basal growth after emerging from the archegonia. The wall of the sporogonium possesses stomata; chlorophyll is present in its cells.

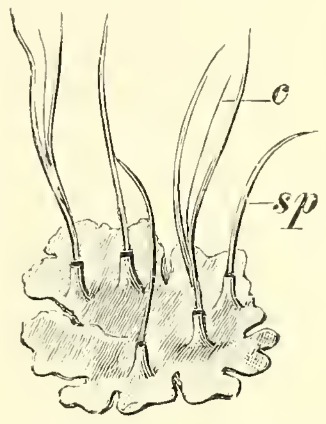


Fig. 322.—*Anthoceros laevis*. *sp*, Sporogonium; *c*, columella. (Nat. size.)

On the under side of the thallus, fissure-like openings, formed by the separation of the cells, lead into cavities filled with mucilage. *Nostoc* filaments penetrate into these cavities, and develop into endophytic colonies.

Order 4. Jungermanniaceae

In the simplest forms of this order the thallus is broadly lobed, similar to that of *Marchantia* (*e.g. Pellia epiphylla*, frequently found on damp ground); or, like that of *Riccia fluitans*, it is narrow and ribbon-shaped, and at the same time profusely branched (*e.g. Metzgeria furcata*, Fig. 162, p. 147). In the other forms, again, the broad, deeply-lobed thallus has an evident midrib, and its margins, as in the case of *Blasia pusilla* (Fig. 11, p. 14), exhibit an incipient segmentation into leaf-like members. The majority of *Jungermanniaceae*, however, show a distinct segmentation into stem and leaflets. The latter consist of one layer of cells without a midrib, and are inserted with obliquely directed laminæ in two rows on each flank of the stem. Some species (*e.g. Frullania Tamarisei*, a delicately branched Liverwort of a brownish colour occurring on rocks and tree-trunks) have also a ventral row of small scale-like leaves, amphigastria (Fig. 323, *a*). The dorsal leaves are frequently divided into an upper and lower lobe. In species growing in dry places, like the previously cited *Frullania*, the lower lobe is modified into a sac, and serves as a capillary water-reservoir. The leaves regularly overlap each other; they are then said to be *succubous*, when the posterior edges of the leaves are overlapped by the anterior edges of those next below (*Frullania*, Fig. 323), or *incubous*, if the posterior edges of the leaves overlap the anterior edges of the leaves next below (*Plagiochila*, Fig. 12, p. 14).

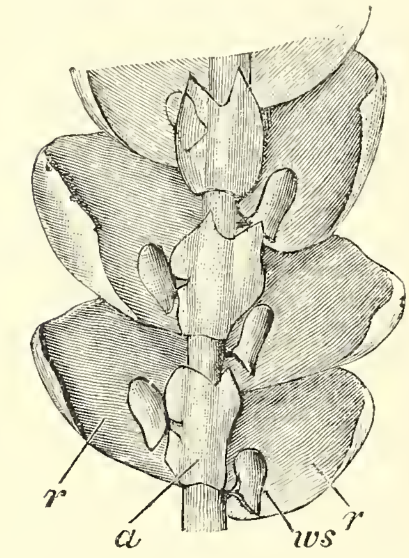


Fig. 323.—Part of a shoot of *Frullania Tamarisci*, seen from below. *r*, Dorsal leaves with the lower lobes (*ws*) modified as water-sacs; *a*, amphigastrium. (× 36.)

The branching stems of the foliose *Jungermanniaceae* are either prostrate or partially erect, and in consequence of the manner in which the leaves develop, present a distinctly dorsiventral appearance.

The long-stalked sporogonium is also characteristic of this order; it is already fully developed before it is pushed through the apex of the archegonial wall by the elongating stalk. It has a spherical capsule which on rupturing splits into four valves (Figs. 11, 12). No columella is formed in the capsule; but in addition to spores it always produces elaters, which by their movements while drying scatter the spores. The stalk of the capsule is delicate. The wall of the capsule (usually two or several cells thick) consists of cells with annular or spiral thickenings, or the walls are uniformly thickened with the exception of the outermost walls. Dehiscence is dependent on the cohesive power of the water in these cells causing the outer walls to bulge into the cavity.

The sporogonia are sometimes situated on the dorsal side of the thallus or stem, and are encircled at the base by an involucre, a sheath-like outgrowth of the thallus or stem (*e.g. Blasia pusilla*, Fig. 11). In other cases the sporogonia arise apically from the extremities of the stem or its branches, and are surrounded by a perianth formed of special, characteristically-shaped leaves (Fig. 12). The majority of the *Jungermanniaceae* resemble the true Mosses; they are small and grow on the ground or on tree-trunks, and in the tropics also on the leaves of forest plants.

CLASS II

Musci (Mosses) (63)

The profusely-branched protonema of the Mosses appears to the naked eye as a felted growth of fine, green filaments (Fig. 316). Buds are developed on the protonema, which grow by means of a three-sided apical cell, and give rise to Moss plants, which always exhibit segmentation into stem and leaves. The leafy Mosses may be readily distinguished from the foliose *Jungermanniaceae* by the spiral arrangement of their small leaves, which are rarely arranged in two rows. In Mosses which have prostrate stems, the leaves, although arranged spirally, frequently assume a somewhat outspread position, and all face one way, so that in such cases a distinction between an upper and a lower side is manifested, but in a manner different from that of the Liverworts.

The STEM OF THE MOSS PLANT is formed of cells which become gradually smaller and thicker-walled towards the periphery. In the stems of many genera (*e.g. Mnium*, Fig. 160) there is found a central, axial strand consisting of elongated, conducting cells with narrow lumina. These strands are not as highly differentiated as the vascular bundles of Pteridophytes. They do not occur, for instance, in the genus *Sphagnum*, which grows in swampy places. The stems of this Moss show a peculiar development of the outer cortical layers (Fig. 324, *C*). The cells in these layers are devoid of protoplasm, and are in communication with each other and the atmosphere by means of large, open pores; to secure rigidity, they are also provided with spirally thickened walls. They have a remarkable power of capillary absorption, and serve as reservoirs for storing and conducting water.

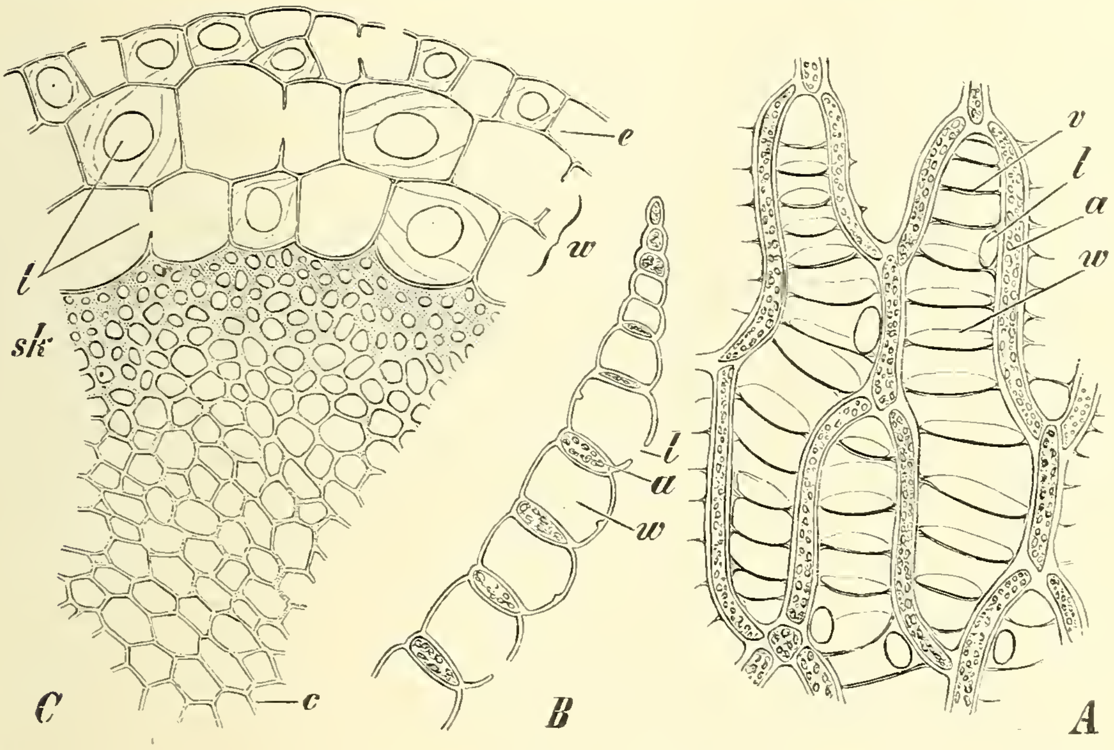


FIG. 324.—*A*, Surface view of a portion of a leaf of *Sphagnum cymbifolium* (× 300); *B*, part of a transverse section of a leaf of *Sphagnum fimbriatum*; *a*, cell containing chlorophyll; *w*, capillary cell; *v*, thickening bands; *l*, pore; *C*, part of a transverse section of the stem of *Sphagnum cymbifolium*; *c*, central cells; *sk*, sclerenchymatous cortical cells; *w*, capillary cells with pores (*l*); *e*, epidermis. (× 120.)

The LEAVES of the true Mosses have, as a rule, a very simple structure. They consist usually of a single layer of polygonal cells containing chloroplasts (Fig. 63 and Fig. 99, *Funaria*), and are generally provided with a conducting bundle of elongated cells (cf. p. 104). The leaves of the Bog Mosses (*Sphagnaceae*) have no bundles, and instead are supplied with capillary cells for the absorption and storage of water. These cells are devoid of protoplasm, and are similar to those in the periphery of the stem, but larger and more elongated; their walls, which are perforated, are strengthened by transverse thickening bands (Fig. 324, *A*, *B*).

Between them are other elongated, reticulately united cells containing chloroplasts. A similar differentiation of the leaf cells occurs in a few other Mosses (*e.g. Leucobryum vulgare*).

A more complicated structure of the leaves resulting from their adaptation to the absorption of water is exhibited by *Polytrichum commune*. In this Moss the leaves develop on their upper surface numerous, crowded, vertical lamellæ, one cell thick; these contain chlorophyll and function as assimilatory tissue, while the spaces between the lamellæ serve as reservoirs for the storage of water. In a dry atmosphere the leaves fold together, and thus protect the delicate lamellæ from excessive transpiration.

The RHIZOIDS (Fig. 327, *B*), each of which consists of a single row of cells, spring from the base of the stem. In structure they resemble the protonema, into which they sometimes become converted, and then give rise to new Moss plants.

The SEXUAL ORGANS are always borne in groups at the apices either of the main axes or of small, lateral branches, surrounded by their upper leaves; each group with its involucral leaves constituting a receptacle. The antheridial and archegonial receptacles are sometimes inappropriately referred to as Moss flowers, but they have nothing in common with the true flowers of vascular plants; the involucral leaves, which frequently have a distinctive structure, are also known as the PERICHÆTIA. Between the sexual organs there are usually present a number of multicellular hairs or paraphyses. The Moss plants may be monœcious, in which case both kinds of sexual organs are borne on the same plant either in the same or different receptacles; or diœcious, and then the antheridia and archegonia arise on different plants.

The SPOROGONIUM of the Mosses develops a capsule with an axial COLUMELLA consisting of sterile tissue. The spore-sac surrounds the columella, which accumulates food material and water for the developing spores. Elaters are never formed. Distinctive variations in the mode of development and structure of the capsules are exhibited by the four orders of the Musci: *Sphagnaceae*, *Andreaeaceae*, *Phascaceae*, and *Bryinae*. The *Sphagnaceae* and *Andreaeaceae* are nearest to the Liverworts.

Order 1. Sphagnaceae (64)

The order of the *Sphagnaceae*, or Bog Mosses, includes only a single genus, *Sphagnum*. The Bog Mosses grow in swampy places, which they cover with a thick carpet saturated with water. The upper extremities of the stems continue their growth from year to year, while the lower portions die away and become eventually converted into peat. Of the numerous lateral branches arising from each of the shoots, some grow upwards and form the apical tufts or heads at the summits of the stems; others, which are more elongated and flagelliform in shape, turn downwards and envelop the lower portions of the stem (Fig. 325, *A*). Every year one branch below the apex develops as strongly as the mother shoot, so that the stem thus becomes falsely bifurcated. By the gradual death of the stem from below upwards the daughter shoots become separated from it, and form independent plants. Special branches of the tufted heads, either on the same plants (monœcious) or on different stocks (diœcious), are distinguishable by their different structure and colour ; on these the sexual organs are produced. The male branches give rise, near the leaves, to spherical stalked antheridia, which open at the apices by means of retroflexing valves, and let free the spirally twisted spermatozoids (Fig. 325, *E*, *F*). The archegonia are borne at the tips of the female branches. After fertilisation, the multicellular embryo of a sporogonium (*B*) is produced from the egg-cell. The sporogonium develops a short stalk with an expanded foot (*C*), but remains for a time enclosed by the archegonial wall or calyptra. Upon the rupture of the archegonium, the calyptra persists just as in the *Hepaticae* at the base of the sporogonium. The capsule is spherical and has a dome-shaped columella, which in turn is overarched by a hemispherical spore-sac (*spo*) ; it possesses an operculum, but no peristome. The ripe sporogonium, like that of *Andreaea*, is borne upon a prolongation of the stem axis, the pseudopodium, which is expanded at the top to receive the foot of the stalk. Of the peculiar structure of the leaves and stem cortex a description has already been given (p.385). The protonema of the *Sphagnaceae* is in some respects peculiar. Only a short filament is formed on the germination of the spore, the protonema broadening out almost at once into a flat structure on which the young Moss plants arise.

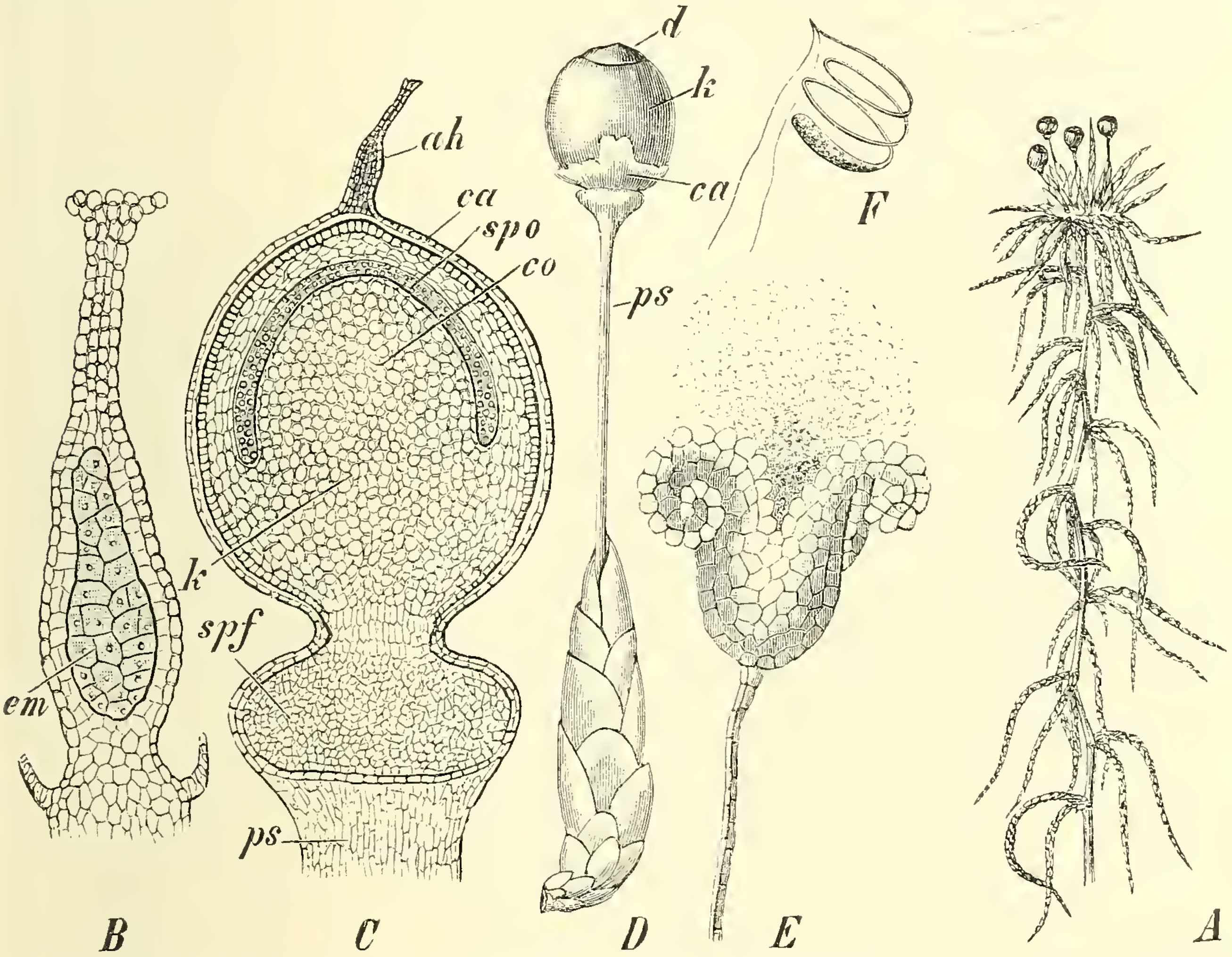


FIG. 325.—*Sphagnum fimbriatum.* *A*, A shoot with four ripe sporogonia. *Sphagnum acutifolium.* *B*, Archegonium with the multicellular embryo of the sporogonium *em* ; *C*, a young sporogonium in longitudinal section ; *ps*, pseudopodium ; *ca*, archegonial wall or calyptra ; *ah*, neck of archegonium ; *spf*, foot of sporogonium ; *k*, capsule ; *co*, columella ; *spo*, spore-sac with spores ; *E*, ruptured antheridium with escaping spermatozoids ; *F*, single spermatozoid, highly magnified. *Sphagnum squarrosum.* *D*, A lateral shoot with a terminal sporogonium ; *ca*, ruptured calyptra ; *d*, operculum. (After W. P. SCHIMPER ; *A*, nat. size ; the other figures magnified.)

Order 2. Andreaeaceae

The *Andreaeaceae* (*Schizocarpae*) comprise only the one genus *Andreaea*, small, brownish cæspitose Mosses growing on rocks. The sporogonium is also terminal in this order. The capsule, at first provided with a calyptra, splits into four longitudinal valves, which remain united at the base and apex (Fig. 326). The stalk is short, and is expanded at the base into a foot (*Spf*), which in turn is borne on a pseudopodium (*ps*), a stalk-like prolongation of the stem resulting from its elongation after the fertilisation of the archegonium.

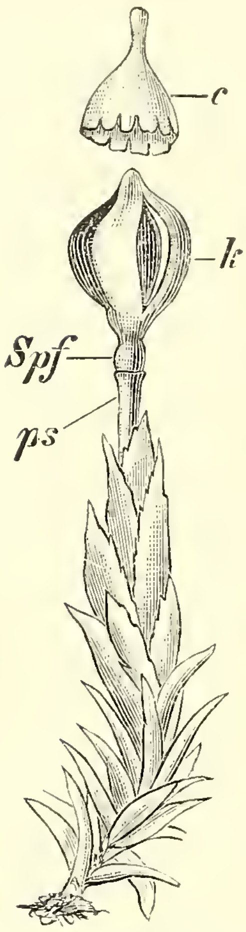


FIG. 326.—*Andreaea petrophila*. *ps*, Pseudopodium; *Spf*, foot; *k*, capsule; *c*, calyptra. (× 12.)

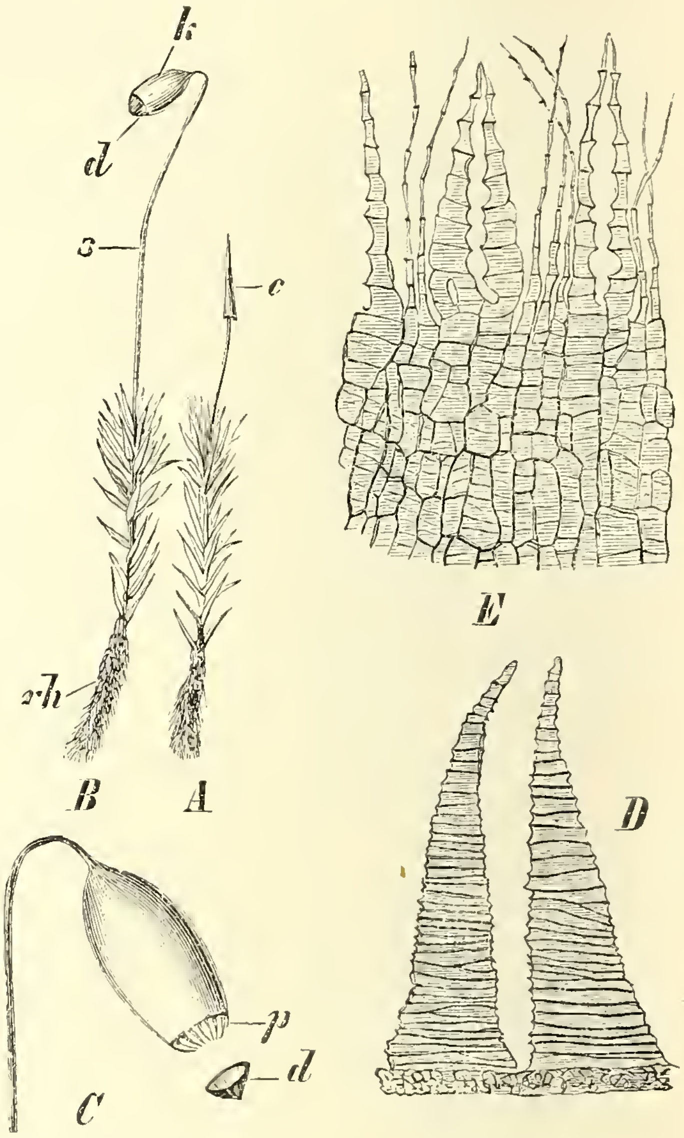


FIG. 327.—*Mnium hornum*. *A*, A plant with sporogonium still bearing a calyptra (*c*); *B*, a plant with ripe sporogonium; *s*, seta; *k*, capsule; *d*, operculum; *rh*, rhizoids; *C*, mature capsule with operculum (*d*) removed; *p*, peristome; *D*, two peristome teeth of the outer row; *E*, part of inner peristome. (*A*, *B* nat. size; *C* × 3; *D*, *E* × 58.)

Order 3. Phascaceae

To the *Phascaceae* (*Cleistocarpae*) belong small Mosses with few leaves growing on the soil; they retain their filamentous protonemata until the capsules are ripe, and have the simplest structure of all the Mosses (Fig. 333). The hooded capsule is terminal and has only a short stalk. It does not open with a lid, but the spores are set free by the decay of its walls.

Order 4. Bryinae (65)

In this order (termed also *Stegocarpae*), which includes the majority of all the true Mosses, the Moss fruit attains its most complicated structure. The ripe SPOROGONIUM, developed from the fertilised egg, consists of a long stalk, the SETA (Fig. 327, *B*, *s*), with a FOOT at its base, sunk in the tissue of the mother plant, and of a CAPSULE (*k*), which in its young stages is surmounted by a hood or CALYPTRA (*A*, *c*). The calyptra is thrown off before the spores are ripe. It consists of one or two layers of elongated cells, and originally formed part of the wall of the archegonium which, at first, enclosed the embryo, growing in size as it grew, until, finally ruptured by the elongation of the seta, it was carried up as a cap, covering the capsule. In the Liverworts the calyptra is, on the contrary, always pierced by the elongating sporogonium, and forms a sheath at its base. The upper part of the seta, where it joins the capsule, sometimes becomes distinctly enlarged and is then termed the APOPHYSIS. In *Mnium* it is scarcely distinguishable, but in *Polytrichum commune* it has the form of a swollen ring-like protuberance (Fig. 329, *ap*), while in species of *Splachnum* it dilates into a large cushion-like structure of a yellow or red colour, upon which the capsule appears only as a small protuberance. The upper part of the capsule becomes converted into a lid or operculum (Fig. 327, *d*), which is sometimes drawn out into a projecting tip. At the margin of the operculum a narrow zone of epidermal cells termed the ring or ANNULUS becomes specially differentiated. The cells of the annulus contain mucilage, and by their expansion at maturity assist greatly in throwing off the lid. In most stegocarpous Mosses the mouth of the dehisced capsule bears a fringe, the PERISTOME, consisting usually of tooth-like appendages.

The peristome of *Mnium hornum* (Fig. 327, *C*, *p*) is double ; the outer peristome is formed of 16 pointed, transversely striped teeth (*D*) inserted on the inner margin of the wall of the capsule. The inner peristome lies just within the outer, and consists of cilia-like appendages, which are ribbed on the inner side and thus appear transversely striped ; they coalesce at their base into a continuous membrane (*E*). Two cilia of the inner peristome are always situated between each two teeth of the outer row. The cilia facilitate the dissemination of the spores by their hygroscopic movements.

The teeth and cilia of the peristome are formed in this instance of thickened portions of the opposite walls of a single layer of cells next to the operculum (Fig. 328), the teeth from portions of the external wall, and the cilia from portions of the internal walls of the same layer. On the opening of the capsule the unthickened portions of this layer break away and the teeth and cilia split apart. The transversely ribbed markings on their surface indicate the position of the former transverse walls.

The structure of the peristome varies greatly in different species of *Bryinae*. By its peculiar form and hygroscopic movements the peristome causes a gradual dissemination of the spores from the capsule.

The central axial portion of the capsule is occupied by the large-celled COLUMELLA. It is completely surrounded by the sporogenous tissue, the so-called spore-sac, which is separated from the wall of the capsule and sometimes also from the columella by loose assimilatory tissue. Stomata occur in the epidermis of the capsule. The Moss fruit, in conformity with its anatomical structure, takes part in assimilation. It ripens slowly outside the archegonium, while the sporogonium of the Liverworts remains enclosed within it until maturity.

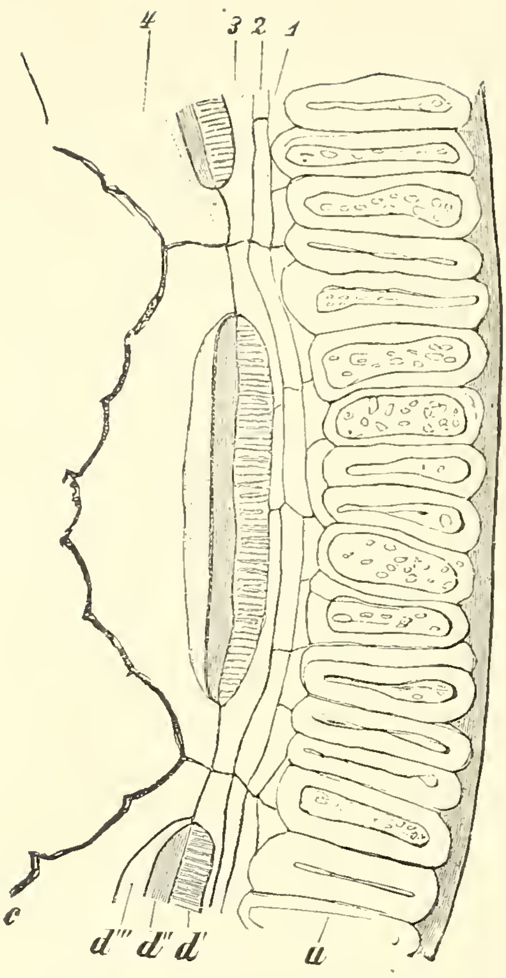


FIG. 328.—*Mnium hornum.* Transverse section through the wall of the capsule in the region of the ring; *a*, cells of the ring; 1-4, successive cell layers with the thickened masses of the inner and outer peristome; *d'*, *d''*, *d'''*, transverse projecting ribs of the coalesced cilia, *c*. (× 240.)

FIG. 329.—*Polytrichum commune.* *rh*, Rhizoids; *s*, seta; *c*, calyptra; *ap*, apophysis; *d*, operculum. (Nat. size.)

FIG. 330.—*Schistostega osmundacea.* *A*, sterile; *B*, fertile plant. (× 5.)

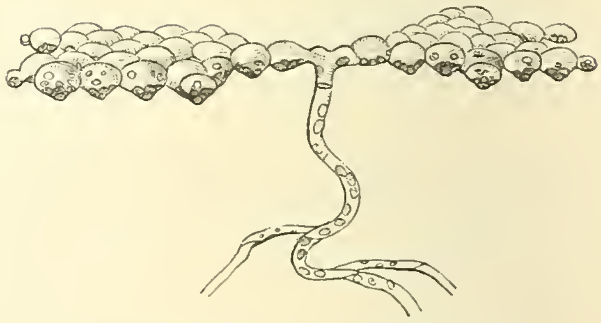


FIG. 331.—Protonema of *Schistostega osmundacea.* (× 90.)

Variations in the form of the capsule, peristome, operculum, and calyptra afford the most important means of distinguishing the different genera. The *Bryinae* are first divided into two sub-orders, according to the position of the archegonia or of the sporogonia developed from them.

(*a*) *Bryinae acrocarpae.*—The archegonia, and consequently the sporogonia, are terminal on the main axis. *Mnium hornum, Polytrichum commune* (Fig. 329), and *Funaria hygrometrica* are common examples. *Schistostega osmundacea*, a moss living in caves, has fertile shoots, which have spirally arranged leaves and bear stalked capsules devoid of peristomes, and also other shoots that are sterile, with two rows of leaves (Fig. 330, *A, B*). The protonema of this species gives out an emerald light (p. 223). Its branched filaments place themselves in a plane perpendicular to the incident rays of light, so that the cells, which are disc-shaped, projecting conically on the under side, reflect the light in the same way as a reflecting mirror (Fig. 331).

FIG. 332.—*Hypnum purum.* (Nat. size.)

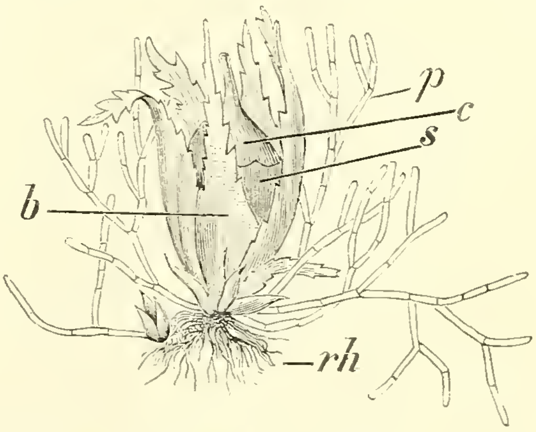


FIG. 333.—*Ephemerum serratum.* *p*, Protonema; *b*, foliage-leaf; *s*, sporogonium; *c*, calyptra; *rh*, rhizoids. (After W. P. SCHIMPER, × 200.)

(*b*) *Bryinae pleurocarpae.*—The growth of the main axis is unlimited, and the archegonia with their sporogonia arise on short, lateral branches (Fig. 332). In this group are included numerous, usually profusely branched species of large Wood Mosses belonging to the genera *Hylocomium, Neckera*, and *Hypnum*, and also the submerged Water Moss, *Fontinalis antipyretica.*

III. PTERIDOPHYTA (VASCULAR CRYPTOGAMS) (61, 66)

The Pteridophytes include the Ferns, Water-Ferns, Horse-tails, and Club Mosses, and represent the most highly developed Cryptogams. In the development of the plants forming this group, as in the Bryophyta, a distinct alternation of generations is exhibited. The first generation, the sexual, bears the antheridia and archegonia; the second, the asexual, develops from the fertilised egg and produces asexual, unicellular spores. On germination the spores in turn give rise to a sexual generation. Both the sexual and asexual generations of the Pteridophyta present marked variations in the mode of their development.

The SEXUAL GENERATION is termed the PROTHALLIUM or

GAMETOPHYTE. It never reaches any great size, being at most a few centimetres in diameter; in some forms it resembles in appearance a simple, thalloid Liverwort; it then consists of a small green thallus, attached to the soil by rhizoids springing from the under side (Fig. 334, *A*). At other times the prothallium is branched and filamentous; sometimes it is a tuberous, colourless mass of tissue, partially or wholly buried in the ground, and leading a saprophytic existence, while in certain other divisions of the Pteridophyta it undergoes reduction and remains more or less completely enclosed within the spore. On the prothallia arise the sexual organs, antheridia (Fig. 340), producing numerous ciliate, usually spiral spermatozoids, and archegonia (Fig. 341), in each of which is a single egg-cell. As in the Mosses the presence of water is necessary for fertilisation.

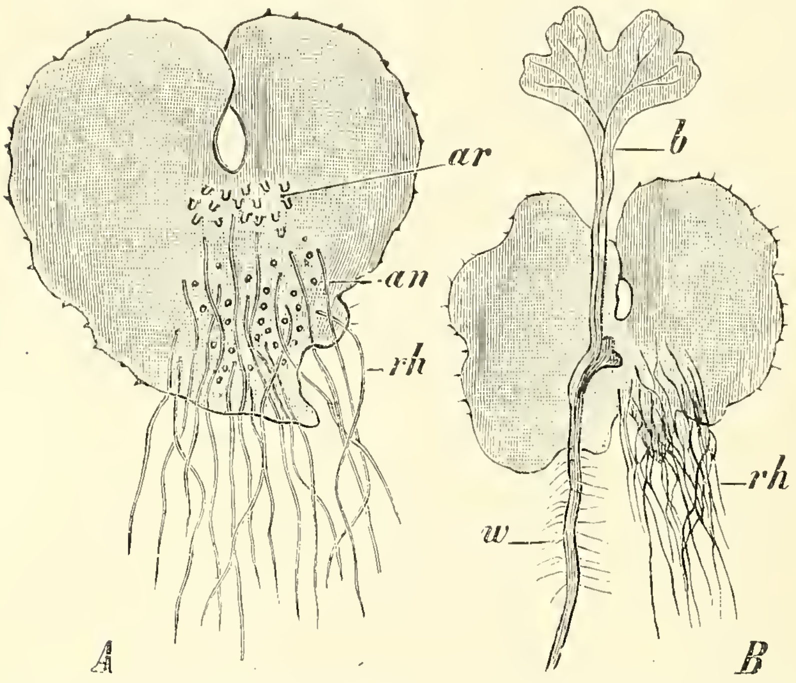


FIG. 334.—*Aspidium filix mas.* *A*, Prothallium seen from below; *ar*, archegonia; *an*, antheridia; *rh*, rhizoids; *B*, prothallium with young Fern attached to it by its foot; *b*, the first leaf; *w*, the primary root. (× circa 8.)

After fertilisation the egg-cell develops into a multicellular embryo, which becomes the asexual generation, as in the Bryophyta. The Bryophyta and Pteridophyta have accordingly been classed together as *Embryophyta* by ENGLER, and termed *Embryophyta zoidiogama*, because the male cells are developed as spermatozoids.

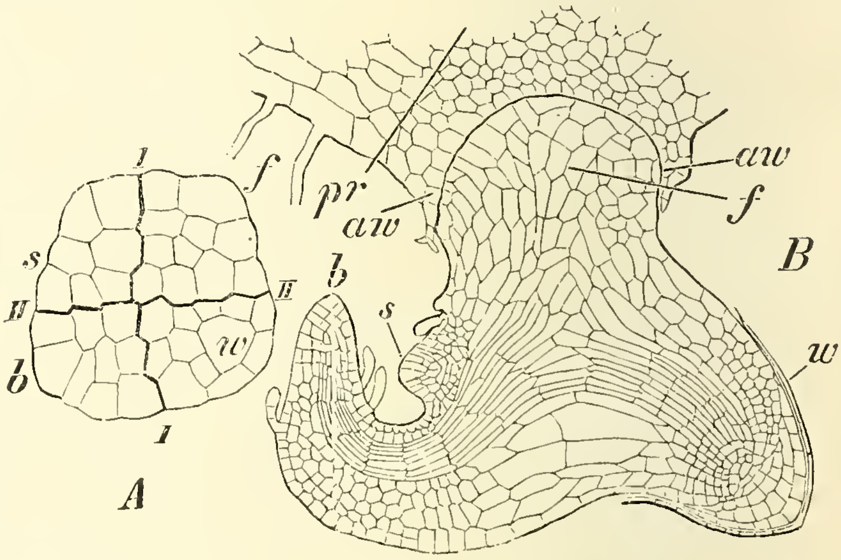


FIG. 335.—*A*, *Pteris serrulata*, embryo freed from the archegonium, in longitudinal section (after KIENITZ-GERLOFF): I, basal wall; II, transverse wall dividing the egg-cell into quadrants, rudiment of the foot *f*, of the stem *s*, of the first leaf *b*, of the root *w*; *B*, section of a further-developed embryo of *Pteris aquilina* (after HOFMEISTER); *f*, foot still embedded in the enlarged venter of the archegonium *aw*; *pr*, prothallium. (Magnified.)

The asexual generation or sporophyte is represented by a plant possessing a highly differentiated internal structure, and externally segmented into stem, leaves, and roots. In the majority of Pteridophytes, the fertilised egg-cell, while still in the archegonium, surrounds itself with a cell wall and undergoes division, first into two cells, by the formation of a transverse or basal wall, and then into octants by two walls at right angles to each other and to the basal wall. By the further division of these eight cells the half above the basal wall gives rise to the tissues of the stem apex and the first leaf, while from the half below the basal wall is produced the primary root, and an organ peculiar to the Pteridophytes, the so-called FOOT (Fig. 335, *f*). The foot is a mass of tissue, by means of which the young embryo remains attached to the parent prothallium and absorbs nourishment from it, until, by the development of its own roots and leaves, it is able to nourish itself independently. The prothallium then usually dies. The stem developed from the embryonic rudiment may be either simple or bifurcated, erect or prostrate; it branches without reference to the leaves, which are arranged spirally or in whorls, or occupy a dorsiventral position. Instead of rhizoids, true roots are produced, as in the Phanerogams (cf. Fig. 166). The leaves also correspond in structure with those of the Phanerogams. Stems, leaves, and root are traversed by well-differentiated vascular bundles, and the Pteridophytes are, in consequence, designated Vascular Cryptogams. The bundles are for the most part constructed after a special type (cf. Figs. 124, 129, 130). Secondary growth in thickness, resulting from the activity of a special cambium, occurs only occasionally in existing forms, but it was characteristic of the stems of certain extinct groups of Pteridophytes.

The SPORES are produced vegetatively in special receptacles termed SPORANGIA, which occur on the asexual generation, either on the leaves, or less frequently on the stems in the axils of the leaves. The sporiferous leaves are termed SPOROPHYLLS. The sporangium consists of a wall composed of several layers of cells enclosing the sporogenous tissue, the cells of which, becoming rounded off and separated from each other as spore mother cells, give rise each to four tetrahedral spores (spore-tetrads). The cells of the innermost layer of the sporangial wall are rich in protoplasm, and constitute the TAPETUM. This layer persists in the *Lycopodineae*, but in the case of the Ferns the walls of the tapetal layer become dissolved. In the course of the development of a sporangium the tapetal cells then wander in between the spore mother cells, so that the spores eventually lie embedded in a mucilaginous protoplasmic mass, the PERIPLASM, from which they derive nourishment. Only the outermost layer of the wall is retained by the mature sporangium. The spores are all unicellular. Each spore has a wall composed of several coats.

The spores of the majority of the Pteridophytes have all the same structure, and give rise on germination to a prothallium, which produces both antheridia and archegonia. In certain cases, however, the prothallia are diœcious. This separation of the sexes extends in some groups even to the spores, which, as MACROSPORES, developed in MACROSPORANGIA, give rise only to female prothallia; or as MICROSPORES, which are produced in MICROSPORANGIA, develop similarly only male prothallia. In accordance with this difference in the spores, a distinction may be made between the HOMOSPOROUS and HETEROSPOROUS forms of the same group; but this distinction has no systematic value in defining the different groups themselves, as it is manifested to an equal degree in groups in other respects quite distinct.

Compared with the Bryophyta, the asexual cormophytic generation of the Pteridophytes corresponds to the sporogonium, the prothallium, on the other hand, to the Moss plant with its protonema; although both groups may have originated phylogenetically from a common ancestor, they have followed altogether different directions in the course of their further development. The correspondence in the structure of their sexual organs, in particular, points to the existence of a relationship between them; on the other hand, their asexual generations exhibit the greatest disagreement, so that it would not seem admissible to regard the asexual generation of the Pteridophytes as derived from the sporogonium of the Mosses, although it is manifestly homologous with it.

The existing Pteridophyta are classified as follows:—

1. *Filicinae.*—Ferns. Stem simple or branched, with well-developed, alternate, often deeply divided or compound leaves. Sporangia either on the under side of the sporophylls, united in sori or free, or enclosed in special segments of the leaves.

Order 1. *Filices.*—Ferns, in the narrower sense. Homosporous.
Order 2. *Hydropterideae.*—Water-Ferns. Heterosporous.

2. *Equisetinae.*—Horse-tails. Stem simple or verticillately branched, with whorled, scale-like leaves forming a united sheath at each node. Sporophylls shield-shaped, bearing the sporangia on the under side, and aggregated into a cone at the apex of each fertile shoot.

Order 3. *Equisetaceae.*—Horse-tails. Homosporous.

3. *Lycopodinae.*—Club Mosses. Stems elongated, dichotomously branched, either forked or forming a sympodium, with leaves, in many cases greatly reduced, or shortened and tuberous with awl-shaped leaves. Sporangia arising singly in the form of firm-walled capsules either from the stem in the leaf-axils, or from the leaf-base.

Order 4. *Lycopodiaceae*—Club Mosses. Homosporous.
Order 5. *Selaginellaceae.*—Heterosporous.
Order 6. *Isoetaceae.*—Heterosporous.

There are also various fossil groups, some of which are included in the above divisions, while some form independent orders.

CLASS I

Filicinae (Ferns)

Order 1. Filices (67)

The *Filices* (True Ferns) constitute the larger part of the Vascular Cryptogams. They comprise a large number of genera with numerous species, being widely distributed in all parts of the world. They attain their highest development in the tropics. The Tree-Ferns (*Cyathea*, *Alsophila*, etc.), which include the largest representatives of the order, occur in tropical countries, and characterise the special family of the *Cyatheaceae*. The stem of a Tree-Fern (Fig. 337) is woody and unbranched ; it bears at the apex a rosette of pinnately compound leaves or fronds, which are produced in succession from the terminal bud, and leave, when dead, a large leaf scar on the trunk. The stem resembling that of a Palm in habit, it is attached to the soil by means of numerous adventitious roots.

The majority of Ferns, however, are herbaceous, and possess a creeping rhizome, terminating usually in a rosette of pinnate or deeply divided leaves. Such a habit and growth are illustrated by the common Fern *Aspidium filix mas*, the rhizome of which is officinal. When young, the leaves (fronds) of this Fern are coiled at the tips (Fig. 336, 1, *a*), a peculiarity common to the Ferns as a whole, and to the Water-Ferns. Unlike the leaves of Phanerogams, those of the Ferns continue to grow at the apex until their full size is attained. The leaves of the common *Polypodium vulgare* are pinnate, and spring singly from the upper side of the branched rhizome, which creeps amongst Moss or on rocks. In other cases the leaves may be simple and undivided, as in the Hart's-Tongue Fern, *Scolopendrium vulgare*.

In the tropics many herbaceous Ferns grow as epiphytes on forest trees.

Peculiar brownish scales (paleae, ramenta), often fringed and consisting of a single layer of cells, invest the stems, petioles, and sometimes also the leaves of most Ferns. These are morphologically trichomes.

The sporangia are generally produced in large numbers, on the under side of the leaves. The sporophylls, as a rule, resemble the sterile, foliage leaves. In a few genera a pronounced heterophylly is exhibited : thus, in the Ostrich Fern, *Struthiopteris germanica*, the dark-brown sporophylls are smaller and less profusely branched, standing in groups in the centre of a rosette of large foliage leaves.

In the different families, differences in the mode of development, as well as in the form, position, and structure of the SPORANGIA, are manifested.

Fig. 336.—*Aspidium filix mas.* 1, Illustration exhibiting general habit; *a*, young leaves: 2, transverse section of rhizome showing the conducting bundles *a*: 3, portion of leaf with sori; *a*, indusium; *b*, sporangia: 4, longitudinal: 5, transverse section of a sorus; *a*, leaf; *b*, indusium; *c*, sporangia: 6, a single sporangium; *a*, stalk; *c*, annulus; *d*, spores. (After Wossidlo. *OFFICINAL.*)

The sporangia of the *Polypodiaceae*, in which family the most familiar and largest number of species are comprised, are united in groups or SORI on the under side of the leaves, at the ends of or between the branches of the nerves. They are borne on a cushion-like projection of tissue termed the RECEPTACLE (Fig. 336, 5), and in many species are covered by a protective membrane, the INDUSIUM, which is an overgrowth of the tissue of the leaf (Fig. 336, 3-5). Each sporangium arises by the division of a single epidermal cell, and consists, when ripe (Fig. 338, *A*), of a capsule attached to the receptacle by a slender multicellular stalk, containing a large number of spores. The wall of the capsule is formed of a single layer of cells. A row of cells with strongly thickened radial and inner walls, extending from the stalk over the dorsal side and top to the middle of the ventral side of

FIG. 337.—*Alsophila crinita.* A Tree-Fern growing in Ceylon. (Reduced.)

the capsule, is specially developed as a ring or ANNULUS, by means of which the dehiscence of the sporangium is effected.

On drying of the wall of the sporangium the cohesion of the remaining water in the cells of the annulus draws in the thin outer walls of these cells; this causes the annulus to shorten and determines the dehiscence of the sporangium by a transverse slit between the broad terminal cells of the annulus. When the pull exerted by the cohesive power of the water gives way, the annulus returns by its own elasticity to its original position, thus effecting the dispersal of the spores (cf. p. 247).

The form and insertion of the sori, the shape of the indusium when present, or its absence, all constitute important criteria for distinguishing the different genera. The sori of *Scolopendrium* are linear, and covered with a lip-shaped indusium consisting of one cell-layer. They are so disposed in pairs, on different sides of every two successive nerves, that they appear to have a double indusium opening in the middle. In structure the indusium resembles the epidermis, but the stomata are absent, and the chromatophores are colourless. In the genus *Aspidium*, on the other hand, each sorus is orbicular in form and covered by a peltate or reniform indusium attached to the apex of the placenta. The sori of *Polypodium vulgare* are also orbicular, but they have no indusia. In the common Brake, *Pteris aquilina*, the sporangia form a continuous line along the entire margin of the leaf, which folds over and covers them with a false indusium.

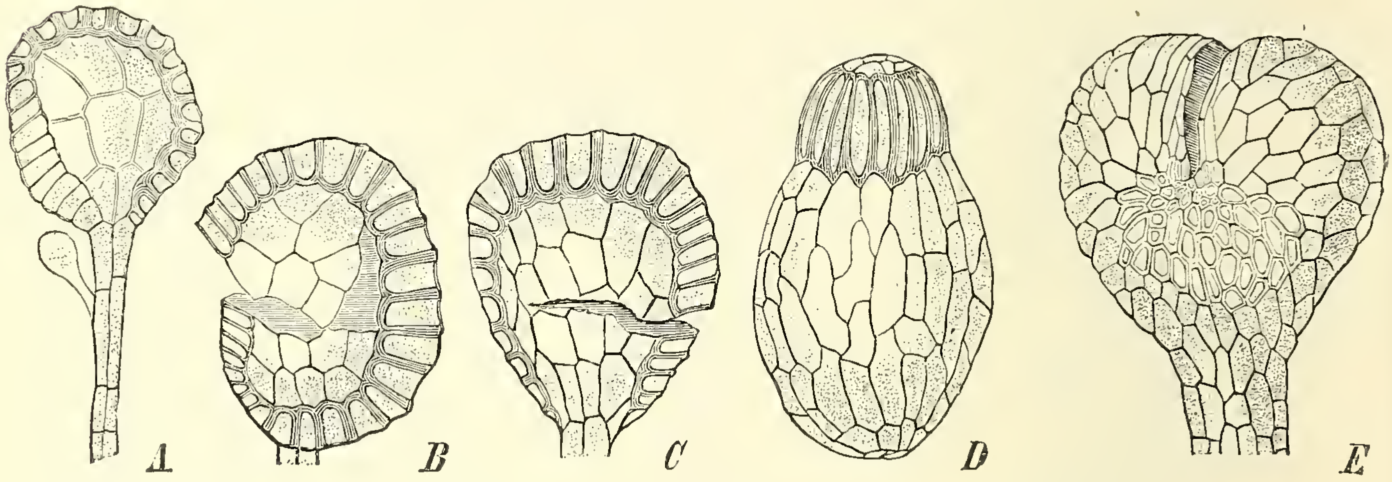


FIG. 338.—Sporangia. *A*, *Aspidium filix mas;* there is a glandular hair at the base; *B* and *C*, *Alsophila armata*, seen from the two sides; *D*, *Aneimia caudata*; *E*, *Osmunda regalis*. (*A-D* × 70 orig.; *E* × 40, after LÜRSSEN.)

Besides the *Polypodiaceae* the Ferns include other families, mainly represented in the tropics, the sporangia of which differ in the construction of the annulus. The sporangia of the *Cyatheaceae*, to which family belong principally the tree-like Ferns, are characterised by a complete annulus extending obliquely over the apex of the capsule (Fig. 338, *B*, *C*). The *Hymenophyllaceae*, often growing as epiphytes on Tree-Ferns, have also sporangia with a complete, oblique, or horizontal annulus. The sporangia of the *Schizaeaceae*, on the other hand, have an apical annulus (Fig. 338, *D*), while in the *Osmundaceae*, of which the Royal Fern, *Osmunda regalis*, is a familiar example, the annulus is represented merely by a group of thick-walled cells just below the apex of the sporangium (Fig. 338, *E*).

All the above-mentioned families and some others possess free sporangia developed from a single epidermal cell and having when mature a wall composed of one layer of cells. They are classed together as *Filices leptosporangiatae*, in contrast to the *Eusporangiatae*, which include the *Marattiaceae* and *Ophioglossaceae*. In these the sporangia take origin from a group of epidermal and underlying cells; they are thick-walled, not provided with an annulus, and open by a transverse slit.

The *Marattiaceae* are tropical Ferns, with thick, tuberous stems and gigantic fronds, each with two stipules at the base. Their mature sporangia are provided with a stiff and firm many-layered wall, and are either free (*Angiopteris*), or all the sporangia of a sorus are united in an oval, capsule-like body, divided into a corresponding number of chambers.

The *Ophioglossaceae* include but few species. Examples of this family are afforded by *Ophioglossum vulgatum*, Adder's Tongue, and *Botrychium*, Moonwort (Fig. 339). Both have a short stem, from which only a single leaf unfolds each year. The leaves in both cases are provided with leaf-sheaths, and peculiarly divided into fertile and sterile segments. In *Ophioglossum* the sterile leaf-like segment is tongue-shaped, the fertile segment narrow and cylindrical, bearing the sporangia in two rows sunk in the tissue. The sterile portion of the leaf of *Botrychium* is pinnate, while the fertile segment is pinnately branched, and thickly beset on the inner side with large nearly spherical sporangia.

All the members of the *Filices* are homosporous. The PROTHALLIUM has usually the form of a flat, heart-shaped thallus (Fig. 334), bearing the antheridia and archegonia on the under side; but in *Botrychium* it is represented, on the contrary, by a small subterranean tuberous body which is saprophytic, and produces the sexual organs on the upper side. In certain *Hymenophyllaceae* (*Trichomanes*), on the other hand, the prothallium is filiform and branched, resembling in structure the protonema of the Mosses, and producing the antheridia and archegonia on lateral branches.

The ANTHERIDIA and ARCHEGONIA (^{68}) are similarly constructed in nearly all Ferns; those of *Polypodium vulgare* (Figs. 340, 341) may serve as a type. The antheridia are spherical projecting bodies (Fig. 340, *A*, *p*), arising on young prothallia by the septation and further division of papilla-like protrusions from single superficial cells. When mature, each antheridium consists of a central cellular cavity, filled with spermatozoid mother cells, and enclosed by a wall formed of two ring-shaped cells (*A*, 1, 2) and a lid-cell (3). The spermatozoid mother cells are produced by the division of the central cell. They are discharged from the antheridium

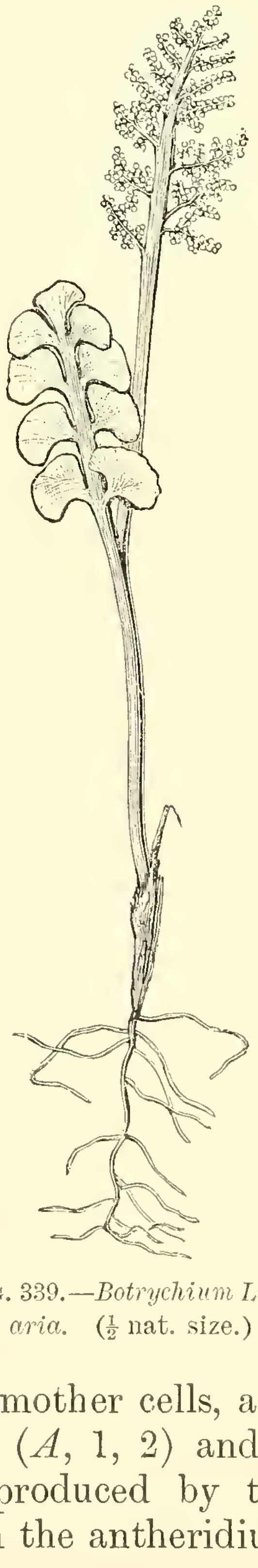


FIG. 339.—*Botrychium Lunaria*. (½ nat. size.)

by the pressure exerted by the swollen ring-cells, and the consequent rupturing of the lid-cell. Each mother cell thus ejected liberates a spirally coiled spermatozoid. The anterior extremity of the spermatozoid is beset with numerous cilia, while attached to its posterior end is a small vesicle which contains a number of granules, and represents the unused remnant of the contents of the mother cell (Fig. 340, *D*, *C*; Fig. 97, *B*).

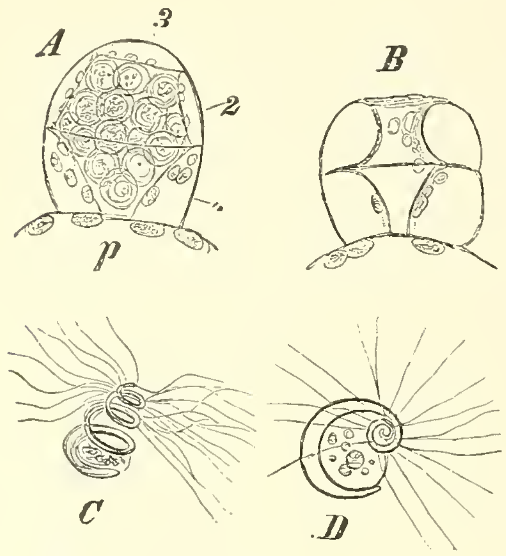


Fig. 340.—*Polypodium vulgare*. *A*, Mature, *B*, discharged antheridium; *p*, prothallium cell; 1 and 2, ring-shaped cells; 3, lid-cell; *C*, *D*, spermatozoids. (*A*, *B* × 240; *C*, *D* × 540.)

The archegonia arise from the many-layered median portion of older prothallia. They are developed from a single superficial cell, and consist of a ventral portion, embedded in the prothallium, and a neck portion. The neck, which projects above the surface of the prothallium, consists of a wall composed of a single layer of cells made up of four cell rows (Fig. 341, *A*, *B*); it encloses the elongated neck-canal-cell.

The ventral portion comprises the large egg-cell and ventral canal-cell immediately above it. As the archegonium matures, the canal-cells become disorganised, and fill the canal with a strongly refractive mucilaginous substance. This swells on the admission of water, and rupturing the neck at the apex is discharged from the archegonium, which is now ready for fertilisation. By means of an acid excretion (malic acid) diffused in the surrounding water the spermatozoids are attracted to the archegonium, and penetrate to the egg-cell. After fertilisation of the egg by one of the spermatozoids, the egg-cell surrounds itself with a cell wall, and without entering upon a condition

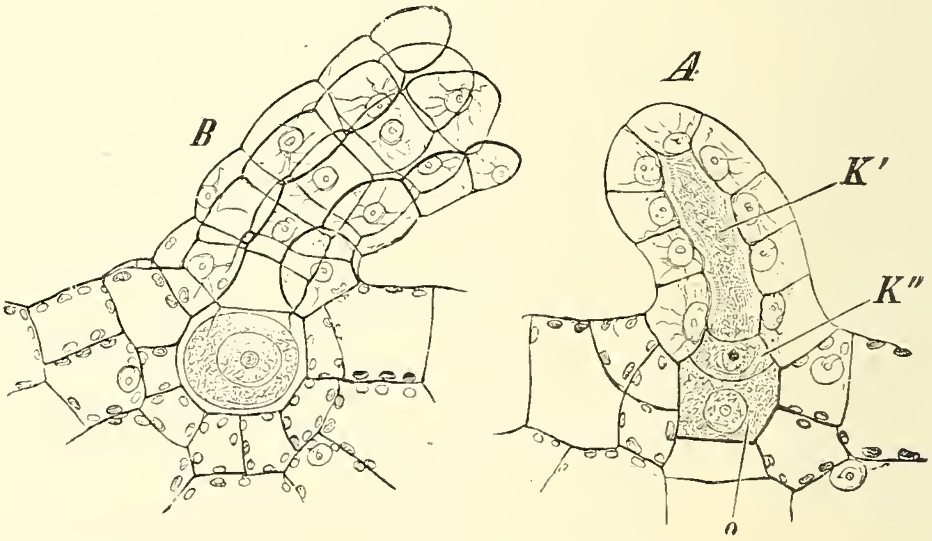


Fig. 341.—*Polypodium vulgare*. *A*, Young archegonium not yet open; *K*′, neck-canal-cell; *K*″, ventral canal-cell; *o*, egg-cell; *B*, mature archegonium, open. (× 240.)

of rest develops into the embryo of the asexual generation, as already described (cf. Fig. 335).

In certain Ferns the sporophyte may originate on the prothallus by a process of budding or direct vegetative growth; the sexual organs are not formed or take no part in the production of the plant (apogamy). Conversely the prothallus may arise directly, without the intervention of spores, from the tissues of the leaf (apospory) (69).

OFFICINAL.—*Aspidium filix mas*, RHIZOMA FILICIS; *Adiantum Capillus Veneris*, FOLIUM ADIANTI s. HERBA CAPILLI VENERIS; *Adiantum pedatum*, FOLIUM ADIANTI. The long silky brown hairs from the base of the leaf-stalks of various Tree-Ferns, especially *Cibotium Barometz*, and other species of this genus, in the East Indies and the Pacific Islands, provide the PALEAE HAEMOSTATICAE used as a styptic (Penawar, Djambi, Pulu).

Order 2. Hydropterideae (Water-Ferns)

The Water-Ferns include only a few genera, which are more or less aquatic in habit, growing either in water or marshy places. They are all heterosporous. The macro- and microsporangia do not develop,

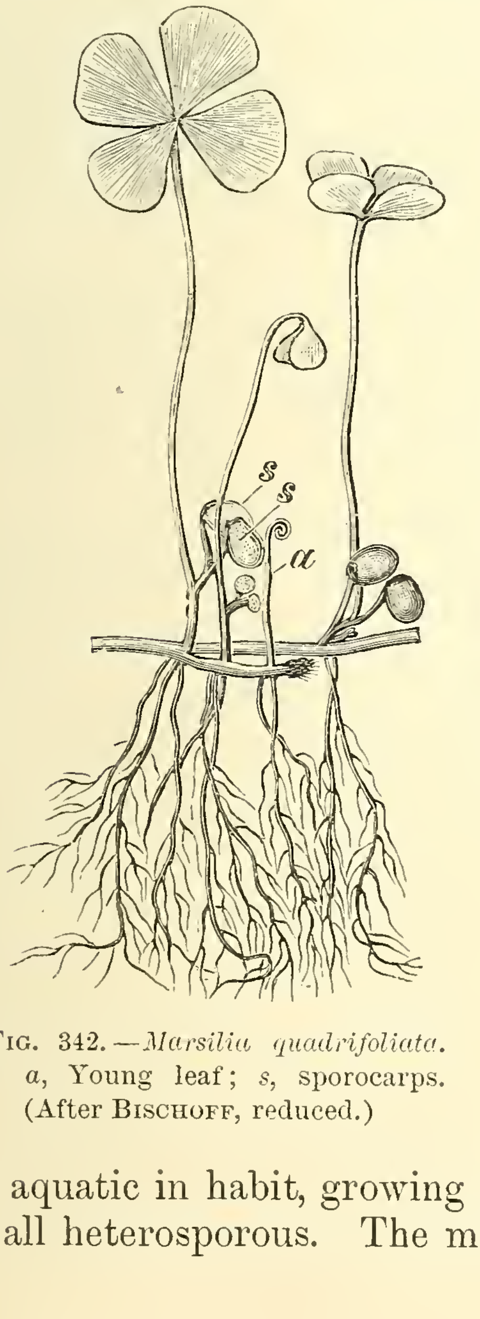


FIG. 342.—*Marsilia quadrifoliata.* *a*, Young leaf; *s*, sporocarps. (After BISCHOFF, reduced.)

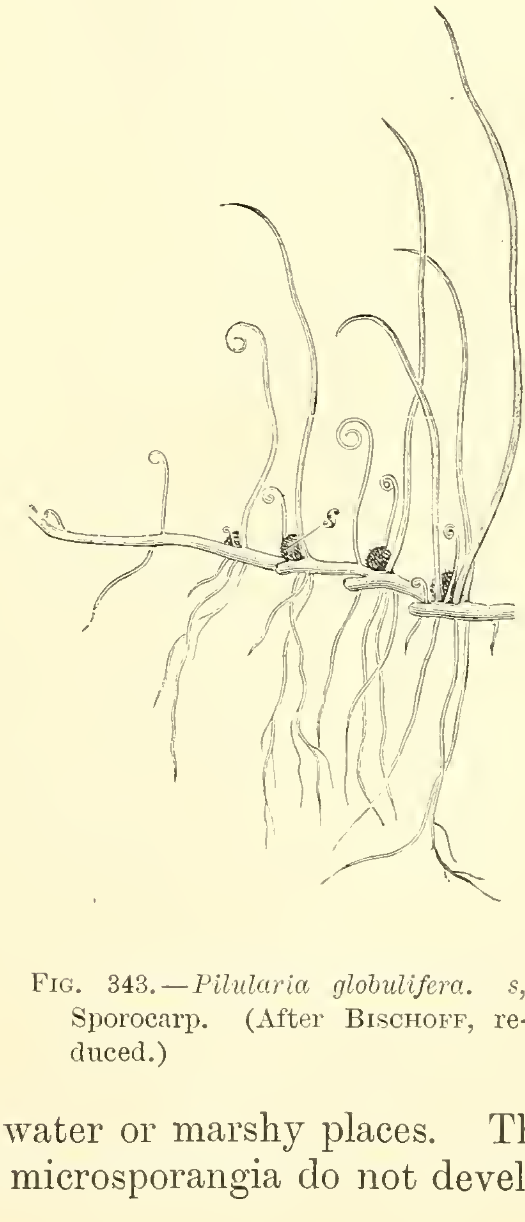


FIG. 343.—*Pilularia globulifera.* *s*, Sporocarp. (After BISCHOFF, reduced.)

like those of the *Filices*, on the under side of the leaves, but are enclosed in special receptacles at their base, constituting sporangial fructifications or sporocarps.

The Water-Ferns are divided into two families, *Marsiliaceae* and *Salviniaceae*, each of which includes two genera.

Marsiliaceae.—Of the two genera belonging to this family the more important is the genus *Marsilia*, comprising about fifty species, of which *M. quadrifoliata* (Fig. 342) may be taken as an example. This species grows in marshy meadows, and has a slender, creeping, branched axis, bearing at intervals single leaves. Each leaf has a long erect petiole, surmounted by a compound lamina composed of two pair of leaflets inserted in close proximity. The stalked oval sporocarps (*s*) are formed in pairs above the base of the leaf-stalk, or in other species they are more numerous ; they represent a fertile leaf-segment corresponding to the bijugate sterile leaf lamina. The sporangia, united in sori, are enclosed within the capsule, disposed in two rows in correspondingly arranged cavities ; in the young fruit each chamber opens outwards on the ventral side by means of a narrow canal, which eventually becomes closed. The sporangia are developed originally, as in the Fern, from superficial cells, but become arched over by the surrounding tissue, and thus subsequently appear as if formed in internal chambers. As Fig. 342 shows, the young leaves, the development of which is as in the *Filices*, are circinate.

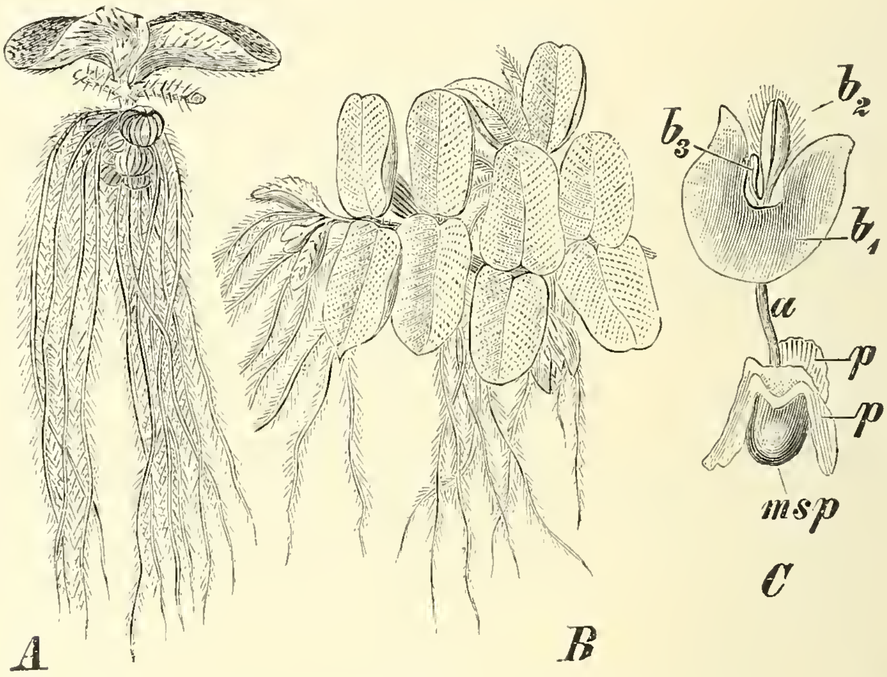


Fig. 344.—*Salvinia natans.* *A*, seen from the side ; *B*, from above (after Bischoff, reduced) ; *C*, an embryonic plant ; *msp*, macrospore ; *p*, prothallium ; *a*, stem ; b_1, b_2, b_3, the first three leaves ; b_1, the so-called scutiform leaf. (After Pringsheim, × 15.)

Pilularia, the second genus included in this family, grows also in bogs and marshes. It differs from *Marsilia* in its simple linear leaves, at the base of which occur the spherical sporocarps, which arise singly from the base of each sterile leaf-segment (Fig. 343).

Salviniaceae.—This family contains only free-floating aquatic plants belonging to the two genera *Salvinia* and *Azolla*. In *Salvinia natans*, as representative of the first genus, the sparingly branched stem gives rise to three leaves at each node. The two upper leaves of each whorl are oval in shape, and developed as floating foliage leaves ; the third, on the other hand, is submerged, and consists of a number of pendent filamentous segments which are densely covered with hairs, and assume the functions of the missing roots. The sporocarps have an entirely different mode of development from that of the *Marsiliaceae;* they are spherical, and are borne in small groups on the submerged leaves at the base of the filamentous segments (Fig. 344). The sporangia are produced within the sporocarp from a column-like receptacle, which corresponds in origin to a modified leaf-segment. The envelope of the sporocarp is equivalent to an indusium ; it arises as a new growth in the form of an annular wall, which is at first cup-shaped, but ultimately closes over the receptacle and its sorus of sporangia.

The second genus, *Azolla,* is chiefly tropical, represented by small floating plants profusely branched, and beset with two-ranked closely crowded leaves. Each leaf consists of two lobes, of which the upper floats on the surface of the water, while the lower is submerged. A small cavity enclosed within the upper lobe, with a narrow orifice opening outwards, is always inhabited by filaments of an Alga (*Anabaena*). From the fact that hairs grow out of the walls of the cavity between the algal filaments, the existence of a symbiotic relation between the two plants would seem to be indicated. Unlike *Salvinia, Azolla* possesses true roots developed from the under side of the stem. The sporocarps are nearly spherical, and produced usually in pairs on the under side of the first leaf of some of the lateral branches.

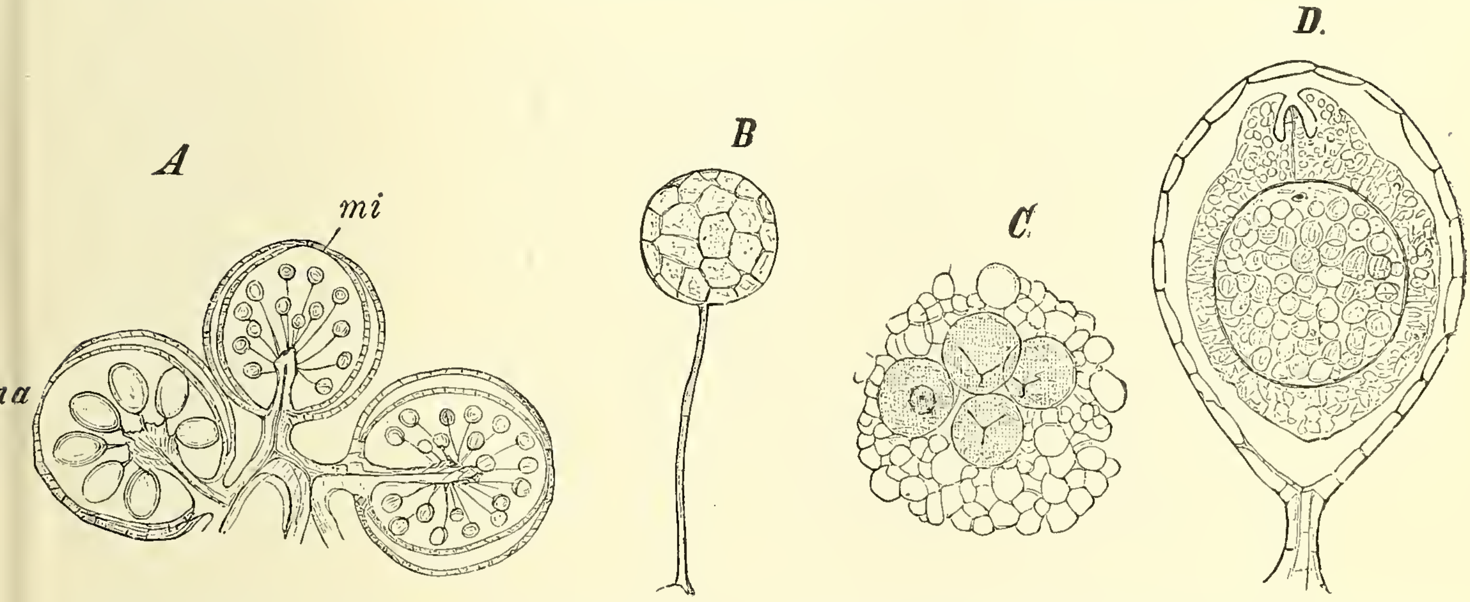


FIG. 345.—*Salvinia natans.* *A*, Three sporocarps in median, longitudinal section ; *ma*, macrosporocarp ; *mi*, microsporocarp (× 8) ; *B*, a microsporangium (× 55) ; *C*, portion of the contents of a microsporangium, showing four microspores embedded in the frothy interstitial substance (× 250) ; *D*, a macrosporangium and macrospore in median longitudinal section (× 55).

In the structure of the sporangia and spores, and in the development of the prothallia, the *Hydropterideae* differ in many respects from the *Filices.* These differences may be best understood on reference to *Salvinia natans* ([70]) as an example. The sporocarps contain either numerous microsporangia or a smaller number of macrosporangia (Fig. 345, *A*, *ma*, *mi*). In structure both forms of sporangia resemble the sporangia of the leptosporangiate Ferns ; they are stalked, and have, when mature, a thin wall of one cell-layer but no annulus (*B*, *D*). The MICROSPORANGIA enclose a large number of microspores, which, as a result of their development in tetrads from the mother cells, are disposed in groups of four (*C*), and embedded in a hardened frothy mass filling the cavity of the sporangium. This frothy interstitial substance is derived from the tapetal cells, which gradually lose their individuality and wander in between the spore mother cells.

The microspores are not discharged, but, while still enclosed within the unruptured microsporangium, each germinating microspore puts out a short tubular male prothallium, which pierces the sporangial wall. The antheridium is developed in this by successive divisions (Fig. 346). Each antheridium produces four spermatozoids, which are set free by the rupture of the cell walls. Although the whole male prothallium is thus greatly reduced, it nevertheless exhibits in its structure a pronounced resemblance to the prothallia of the *Filices*.

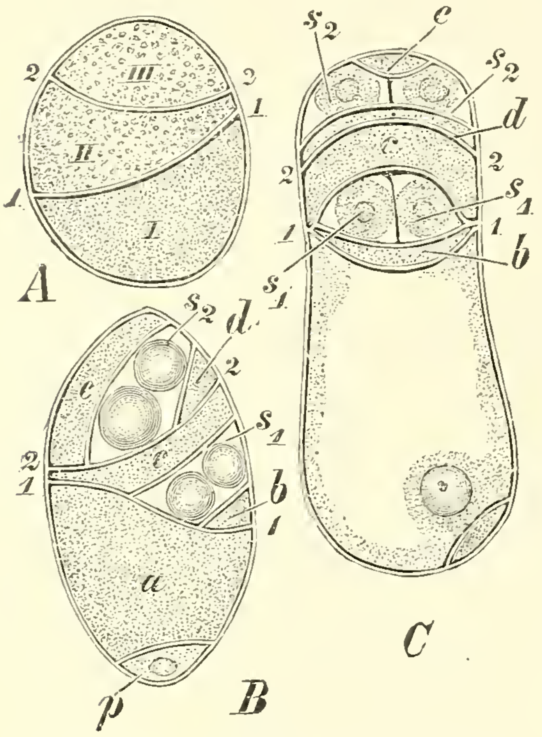


FIG. 346.—*Salvinia natans*. Development of the male prothallium. *A*, Division of the microspore into three cells *I-III* (× 860); *B*, lateral view; *C*, ventral view of mature prothallium (× 640). Cell *I* has divided into the prothallium cells *a* and *p*; cell *II*, into the sterile cells *b*, *c*, and the two cells s_1, each of which has formed two spermatozoid mother cells; cell *III*, into the sterile cells *d*, *e*, and the two cells s_2. The cells $s_1 s_1$ and $s_2 s_2$ represent two antheridia; the cells *b*, *c*, *d*, *e* their wall cells. (After BELAJEFF.)

The MACROSPORANGIA are larger than the microsporangia, but their walls consist similarly of one cell-layer (Fig. 345, *D*). Each macrosporangium produces only a single large macrospore, which develops at the expense of the numerous spores originally formed. The macrospore is densely filled with large angular proteid grains, oil globules, and starch grains; at its apex the protoplasm is denser and contains the nucleus; the membrane of the spore is covered by a dense brown exinium, which in turn is enclosed in a thick frothy envelope, the perinium, investing the whole spore and corresponding to the interstitial substance of the microspores, and also formed from the dissolution of the tapetal cells. The macrospore remains within the sporangium, which is eventually set free from the mother plant. On the germination of the macrospore, a small-celled female prothallium is formed by the division of the denser protoplasm at the apex, while the large underlying cell does not take part in the division, but from its reserve material provides the developing prothallium with nourishment. The spore wall splits into three valves, the sporangial wall is ruptured, and the green prothallium protrudes as a small saddle-shaped body. On it three archegonia are produced, but only the fertilised egg-cell of one of them develops into an embryo, whose foot, remaining for a time sunk in the venter of the archegonia, finally ruptures it (Fig. 347). The first leaf of the germ plant is shield-shaped (Fig. 344, *C*), and floats on the surface of the water.

The development of *Azolla* (^{71}) proceeds in a similar manner, but the sporangia and spores exhibit a number of distinctive peculiarities. The numerous spores of the microsporangia are aggregated into several nearly spherical balls or massulæ, formed from the interstitial substance derived from the protoplasm of the tapetal cells. Each massula, enclosing a number of spores, is beset externally with barbed, hook-like out-growths of the interstitial substance. On the rupture of the sporangia the massulæ are set free in the water, and are carried to the macrospores, to which they hook themselves fast. A sporocarp contains one macrosporangium, in which only a single macrospore comes to maturity; in the course of its development it supplants all the other spore-rudiments, and finally the sporangial wall itself becomes flattened against the inner wall of the sporocarp, frequently undergoing at the same time partial dissolution. The macrospore is enveloped by a spongy perinium whose outer surface exhibits numerous depressions and protuberances prolonged into filaments. At the apex of the spore the perinium expands into three pear-shaped appendages, while the upper part of the ruptured sporangium remains attached to the spore in the form of an umbrella-like expansion. The formation of the prothallia is effected in essentially the same way as in *Salvinia*, except that only one antheridium with eight spermatozoids arises on each of the small male prothallia protruding from a massula.

The sporocarps of the *Marsiliaceae* have a more complicated structure: those of *Pilularia globulifera* are divided into four chambers, each with a single sorus; in *Marsilia* they enclose numerous sori (14-18) disposed in two rows. The sori in both genera contain both micro- and macrosporangia, while those of the *Salviniaceae* are always unisexual.

In the case of the *Marsiliaceae* the prothallia are even more reduced, but otherwise their mode of development is very similar. Each of the minute female prothallia formed at the apices of the macrospores produces a single archegonium.

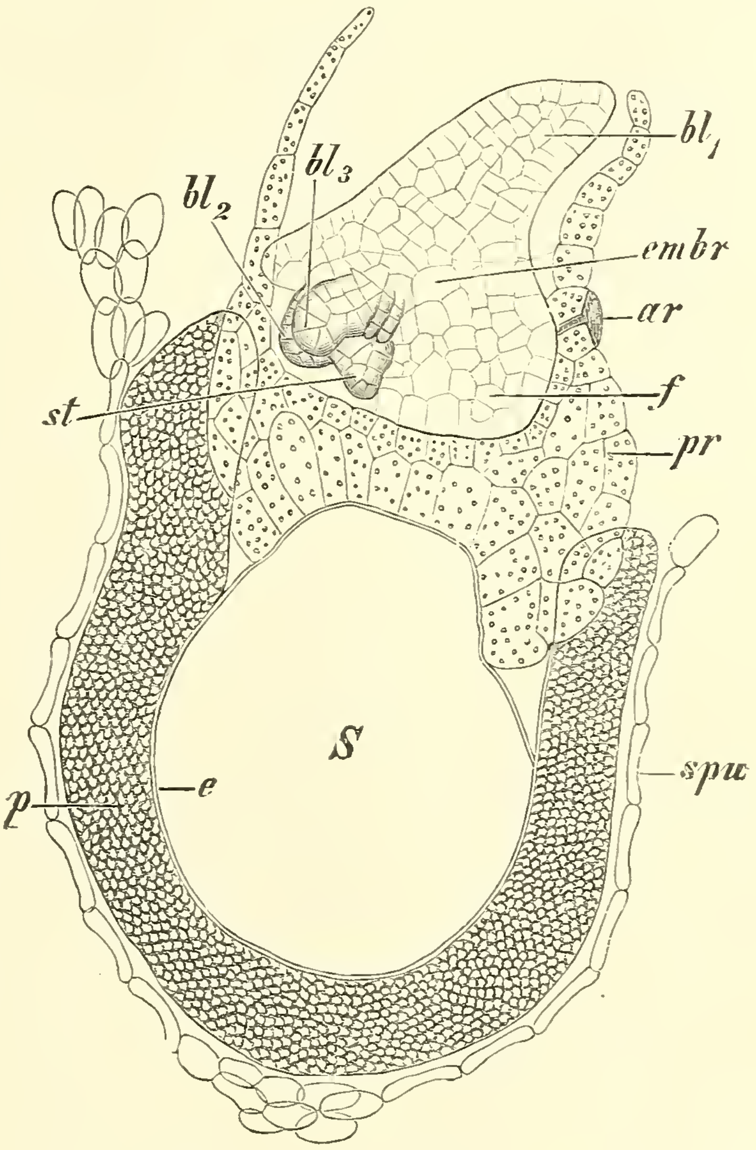


FIG. 347.—*Salvinia natans.* Embryo in longitudinal section; *pr*, prothallium; *S*, spore-cell; *e*, exinium; *p*, perinium; *spw*, sporangial wall; *ar*, archegonium; *embr*, embryo; *f*, foot; bl_1, bl_2, bl_3, the first three leaves; *st*, apex of stem. (After PRINGSHEIM, × 100.)

CLASS II

Equisetinae (Horse-tails) (72)

The *Equisetinae*, which form an entirely independent class, include only the one genus *Equisetum*, comprising 25 species, found widely distributed over the whole world. Developed partly as land, partly as swamp plants, they may always be distinguished by the characteristic structure and habit of the asexual generation. They have a branching, underground rhizome on which arise erect, aerial haulms, usually of annual growth. The rhizome of the common Horse-tail, *Equisetum arvense*, develops also short tuber-like branches which function as reservoirs of reserve material and hibernating organs (Fig. 349, 2, *a*). The aerial haulms remain either simple, or they give rise to branch whorls, and these in turn to whorls of a higher order. Each axis consists of a series of elongated internodes; externally it is channelled by longitudinal furrows, while internally it is traversed by a central air-passage and by a number of smaller peripheral passages, vallecular canals, one opposite each of the furrows. Between the central and vallecular canals, and alternating with the latter, is a circle of bicollateral vascular bundles (Fig. 348).

The leaves of the *Equisetinae*, both in their structure and in the manner of their arrangement on the stem, are also characteristically developed. At each node is borne a whorl of scale leaves pointed at the tips, and united below into a sheath closely enveloping the base of each internode. The leaves of the successive whorls alternate regularly with each other. The lateral branches are developed in the axils of the scale leaves, but not having space to grow upwards they pierce the narrow sheath. As a result of the reduction of the leaf laminæ, the haulms themselves assume the function of assimilation, and for that purpose their cortical tissue under the epidermis is provided with chlorophyll.

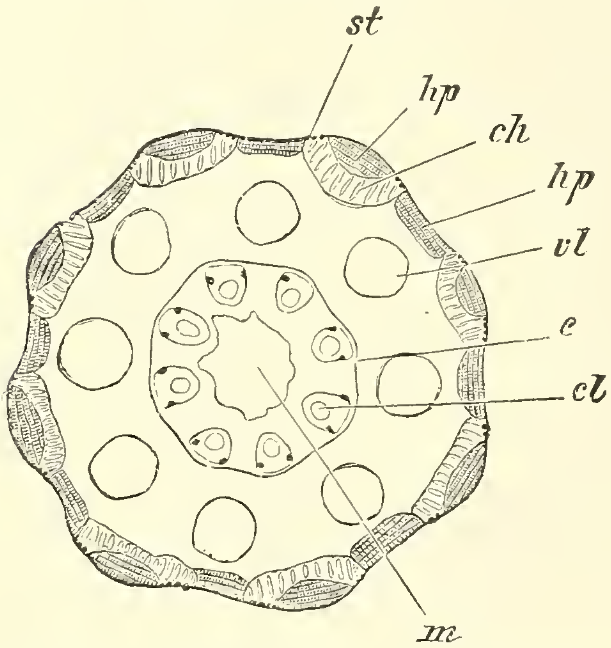


FIG. 348.—*Equisetum arvense.* Transverse section through the stem. *m*, Lysigenic medullary cavity; *e*, endodermis; *cl*, carinal canals in the bicollateral bundles; *vl*, vallecular cavities; *hp*, sclerenchymatous strands in the furrows and ridges; *ch*, tissue of the primary cortex containing chlorophyll; *st*, rows of stomata. (× 11.)

The SPORANGIA are formed of specially shaped leaves or sporophylls. Like the scale leaves the sporophylls are developed in whorls, but are closely aggregated at the tips of the erect fertile shoots into a cone (Fig. 349, 1, *a*), which is sometimes spoken of as a flower, from the correspondence in its structure to the male flower of the Conifers. The lowest whorl is sterile, and forms a collar-like protuberance. The sporophylls (Fig. 349, 3, 4) are stalked and have a shield-shaped lamina, on the under side of which are borne the sac-like sporangia (5-10). In the young sporangium the sporogenous tissue is surrounded by a wall consisting of several cell layers, but eventually the so-called tapetal cells of the inner layers become disorganised, and their protoplasm penetrates between the developing spores. At maturity, the wall of the sporangium consists only of the outermost of the original layers whose cells are provided with annular and spiral thickenings; the sporangia thus resemble the homologous pollen-sacs of Phanerogams. The sporangia split longitudinally, and set free a large number of green spores, which are nearly spherical in shape, and have peculiarly constructed walls. In addition to the intine and exine, the spores are overlaid with a perinium formed from the protoplasm of the tapetal cells, and consisting of two intersecting spiral bands which are attached to the spores only at their point of intersection (Fig. 349, 5-7). On drying, the spiral bands loosen and become uncoiled; when moistened they close again around the spore. By means of their hygroscopic movements they serve to hook together the spores, and in this way is assured the close proximity of the unisexual prothallia which they produce.

In certain species some of the aerial haulms always remain sterile, branching profusely, while others which produce the terminal cones either do not branch at all, or only at a later stage, and then sparingly. This distinction between the sterile and fertile haulms is most marked in *Equisetum arvense* and *Equisetum Telmateja*, in

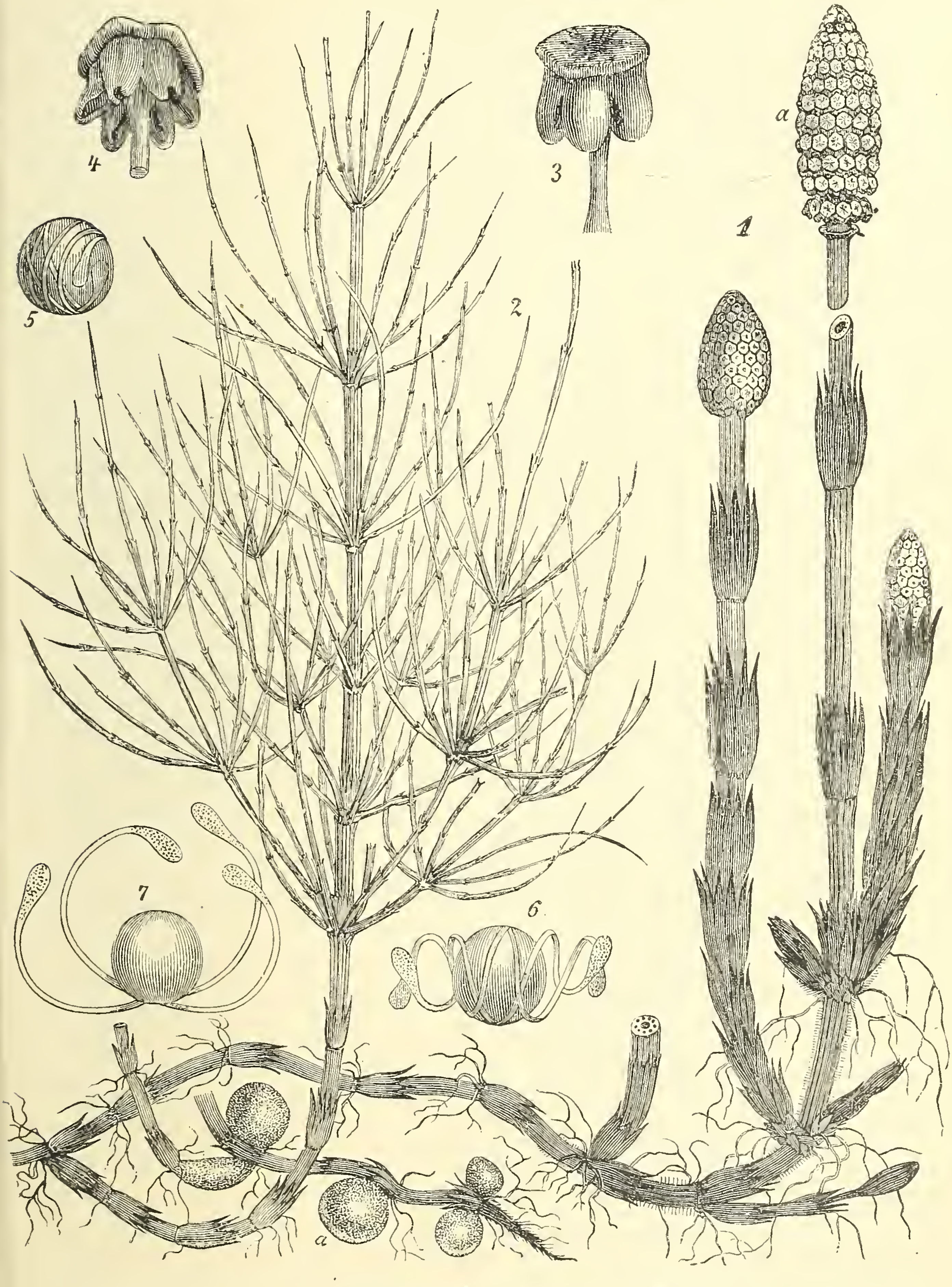


FIG. 349.—*Equisetum arvense*. 1. ~~Fertile haulms~~ terminating in the flower-cones (*a*); 2, a sterile vegetative haulm; *a*, rhizome tubers; 3, sporophyll with sporangia; 4, sporophyll with ruptured sporangia; 5, 6, 7, spores with the spiral bands of the perinium. (After WOSSIDLO.)

both of which the fertile shoots are entirely unbranched, and terminate in a single cone (Fig. 349, 1). Resembling in their mode of life a parasite upon the rhizome, they are otherwise distinguished from the vegetative haulms by their lack of chlorophyll and their light yellow colour.

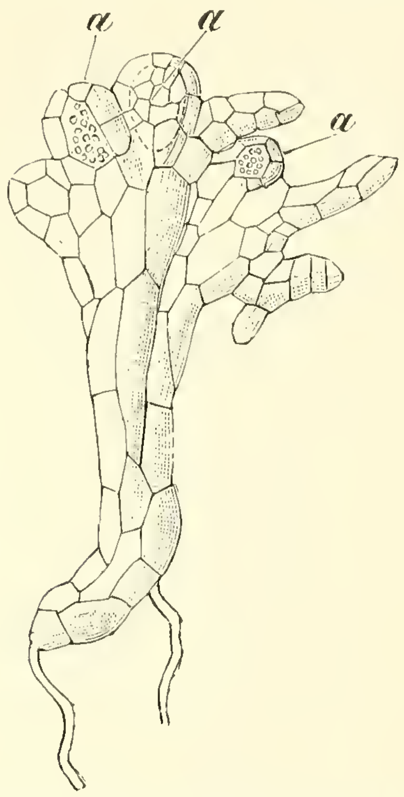


Fig. 350.—*Equisetum arvense.* Male prothallium with three antheridia, *a.* (After Hofmeister, × 200.)

The spores are all of one kind, and on germination give rise to thalloid PROTHALLIA, which are generally diœcious. In the adjoining figure (Fig. 350) a male prothallium of *Equisetum arvense* is represented, showing the first formed antheridia (*a*) somewhat sunk in the tissue. The female prothallia attain a large size, and branching profusely, are prolonged into erect, ruffled lobes at whose base the archegonia are produced. In structure the archegonia resemble those of the Ferns, but the upper cells of the four longitudinal rows of cells constituting the neck are more elongated and, on opening, curve strongly outwards. The development of the embryo corresponds, also, essentially with that of the Fern-embryo, except that the first leaves are arranged in a whorl and encircle the apex of the stem. The growth of the stem is effected by the division of a three-sided apical cell (Figs. 163, 164).

The outer epidermal walls of the stem are more or less strongly impregnated with silica. In *Equisetum hiemale,* and to a less degree in *Equisetum arvense,* the silicification of the external walls is carried to such an extent that they are used for scouring metal utensils and for polishing wood.

Equisetum giganteum, growing in South America, is the tallest species of the genus; its branched haulms, half supported by neighbouring plants, attain a height of over twelve metres.

Class III

Lycopodinae (Club Mosses)

To the *Lycopodinae* belong, as their most important and widely distributed genera, *Lycopodium, Selaginella,* and *Isoetes.* They are distinguished from the other Pteridophyta, of which they resemble most nearly the eusporangiate *Filices,* by their general habit and the mode of their sporangial development.

Unlike the fertile leaves of the *Filicinae* and *Equisetinae,* which always bear numerous sporangia, the sporophylls of the *Lycopodinae* produce the sporangia singly, at the base of the leaves or in their axils. Although in many cases scarcely distinguishable from the sterile leaves, the sporophylls are frequently distinctively shaped, and, like those of *Equisetum,* aggregated at the ends of the fertile shoots into terminal cone-like flowers. Compared with the leaves, the sporangia are relatively large. They are developed in the same way as those of the eusporangiate *Filices* and *Equisetinae*, from a projecting group of cells derived from the epidermis and the underlying tissue; while in the other Pteridophyta the sporangia are developed from a single epidermal cell. The innermost layer of the sporangial wall, the tapetal layer, is not absorbed. The sporangia have no annulus. Except in the case of *Isoetes*, whose spores become free by the decay of the sporangial wall, they dehisce by longitudinal slits, which divide the sporangia into two or more valves; the slits occur where rows of cells of the wall have remained thin. The sporangia of *Lycopodium* are homosporous; those of other *Lycopodinae* heterosporous. The heterosporous forms produce only greatly modified and reduced prothallia; in the genus *Lycopodium*, on the other hand, the prothallia are well developed, exhibiting the most complicated structure known in the sexual generation of Pteridophyta. In the development of their sexual generation the heterosporous *Lycopodinae* resemble in many respects the heterosporous *Hydropterideae*.

The dichotomous branching of the stems and roots is characteristic of this class (Figs. 18, 19, p. 19); in the genus *Isoetes*, however, the stem is unbranched and tuberous.

Order 1. Lycopodiaceae (73)

The numerous, widely distributed species of the genus *Lycopodium* (Club Moss) are for the most part terrestrial plants; in the tropics epiphytic forms also occur. In *Lycopodium clavatum*, one of the commonest species, the stem, which is thickly covered with small, awl-shaped leaves, creeps along the ground; it branches dichotomously, and gives rise to ascending lateral branches, while from the under side spring the dichotomously branched roots (Fig. 351). The flower-cones, consisting of the closely aggregated sporophylls, are situated in groups of two or more at the ends of the forked, erect shoots. The sporophylls are not like the sterile leaves in shape; they are broader and more prolonged at the tip; each bears a large reniform sporangium on the upper side at the base. The sporangium opens into two valves by a transverse slit, and lets free numerous minute spores (Fig. 351, 2).

Lycopodium Selago differs in habit from the other species; its bifurcately-branched stems are all erect, and the flower-cones are not distinct from the vegetative region of the fertile shoots.

The spores of the Lycopodiums are all of one kind, and in consequence of their formation in tetrads are of a tetrahedral though somewhat rounded shape. The exine is covered with a reticulate thickening.

The mode of germination and development of the sexual generation have as yet been determined only for a few species. The prothallia of *Lycopodium clavatum* and the closely related *L. annotinum* are small white tuberous structures, which live as subterranean saprophytes. At first top-shaped, they become converted by the continued marginal growth into cup-shaped lobed bodies, which may attain a size of two centimetres. Long rhizoids spring from the lower surface, while the upper surface bears numerous antheridia and archegonia. In *L. complanatum* the subterranean prothalli are turnip-shaped, in *L. Selago* rounded or elongated and cylindrical. The prothalli of the latter may be developed on the surface of the soil, in which case they are green.

In the case of *L. inundatum*, the prothalli of which are found on damp peaty soil, and in the tropical *L. cernuum* (Fig. 352), with erect profusely-branched shoots, the prothallia are poor in chlorophyll and are attached to the soil by rhizoids; they have the form of small, half-buried, cushion-like masses of tissue which give rise to green aerial thalloid lobes. The archegonia occur at the base of these lobes, the antheridia also on their surface.

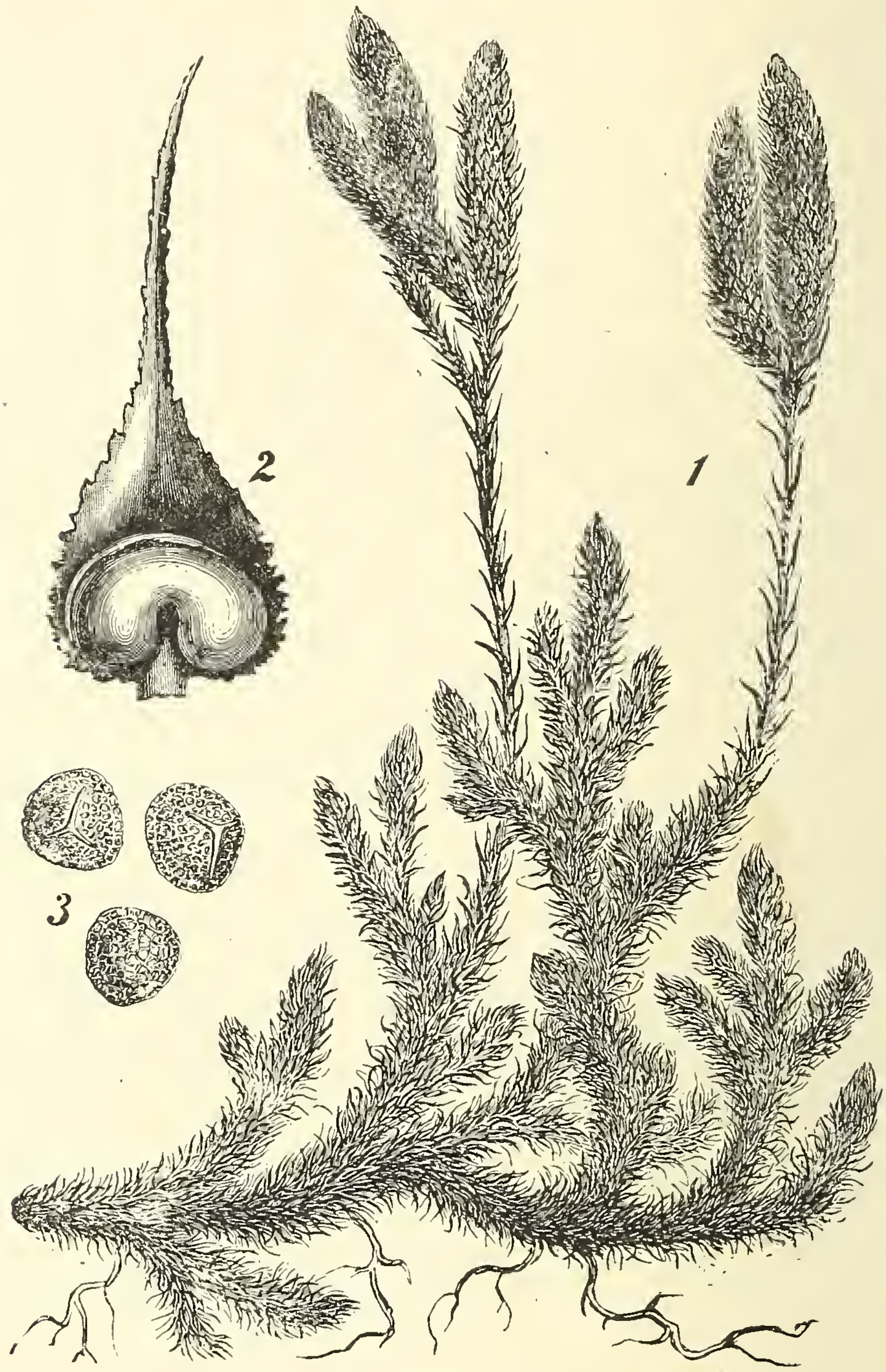


Fig. 351.—*Lycopodium clavatum.* 1, Plant with fertile shoots; 2, scale-like sporophyll with sporangium; 3, spores, highly magnified. (After Wossidlo. *Officinal.*)

The prothallia are all monœcious. The antheridia are somewhat sunk in the tissue (Fig. 352, *C*), and enclose numerous spermatozoid mother cells, in which small biciliate spermatozoids are formed. The archegonia (Fig. 352, *D*) are constructed like those of the Ferns, but have a shorter neck, whose upper cells become disorganised on opening. The number of neck-canal-cells differs in the various species (1, 3, 5, or 6-10).

The embryonic development, which is effected differently from that in the Ferns, agrees closely with that of *Selaginella* (Fig. 357). A SUSPENSOR or EMBRYO-BEARER is developed ; it is not, however, laterally inserted, but occurs on the contrary at the foot end of the embryo, or between the foot and the apex of the stem.

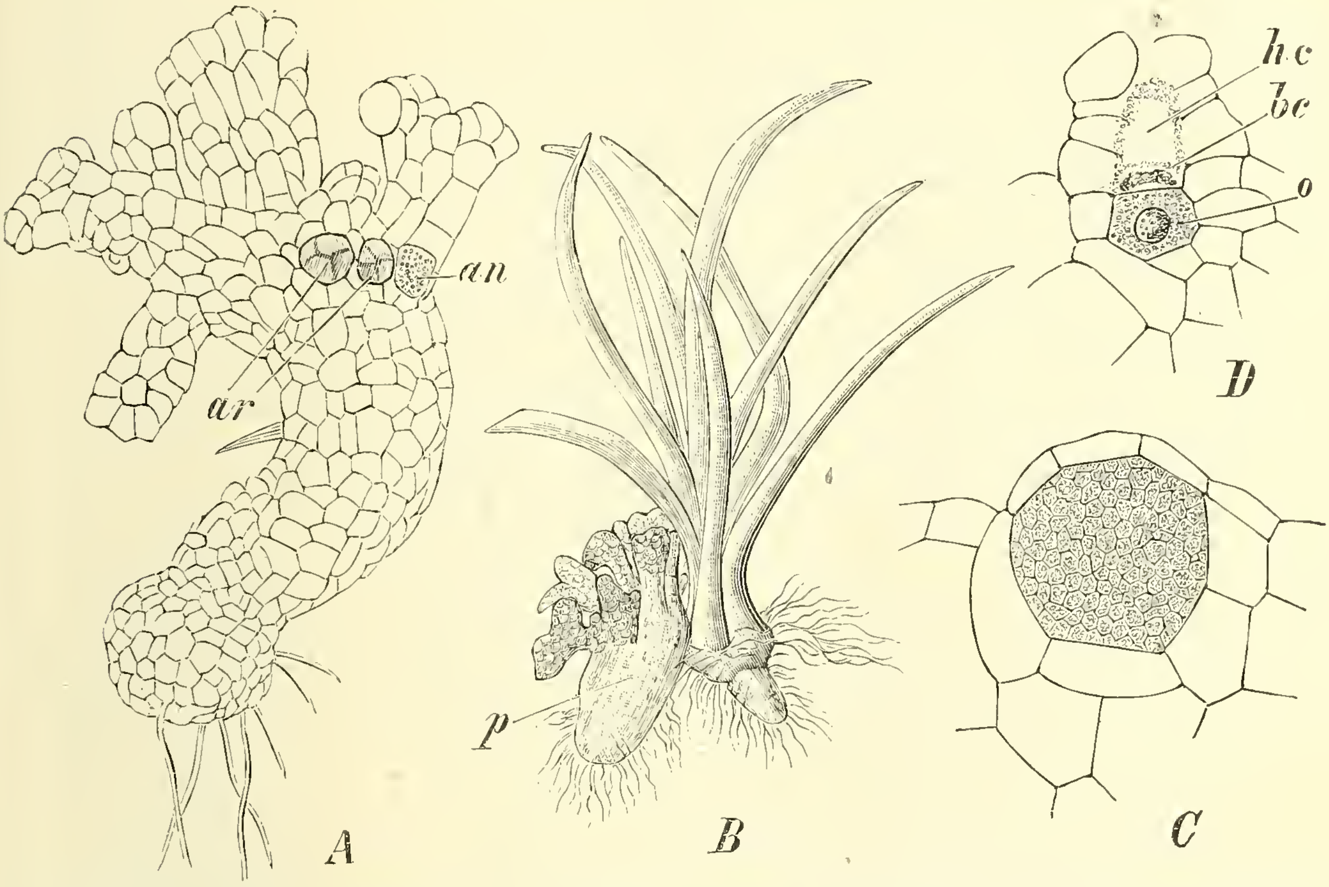


FIG. 352.—*Lycopodium cernuum*. *A*, Prothallium with two archegonia *ar*, and an antheridium *an* (× 70) ; *B*, older prothallium, *p*, with embryonic plants (× 15) ; *C*, section through an antheridium (× 250) ; *D*, archegonium ; *o*, egg-cell ; *bc*, ventral canal-cell ; *hc*, disorganised neck-canal-cell. (After TREUB, × 250.)

OFFICINAL.—LYCOPODIUM, the spores of *Lycopodium clavatum* and other species.

Order 2. Selaginellaceae (^{74})

To this order belongs the genus *Selaginella*, represented by numerous and for the most part tropical species. They have, as a rule, profusely forked, creeping, and sympodially branched stems, but occasionally erect, branched stems ; some form moss-like beds of vegetation ; others, climbing on adjacent plants, possess stems several metres long. In general the Selaginellas are similar in habit to the Lycopodiums. They have small, scale-like leaves which usually exhibit a dorsiventral arrangement, such as is shown, for example, in the Alpine *Selaginella helvetica* (Fig. 353), whose stem is covered with two rows of small dorsal or upper leaves, and opposite to them two rows of larger, ventral or under leaves. The development of a small, membranous ligule at the base of the leaves, on their dorsal side, is characteristic of the Selaginellas.

As in *Lycopodium*, the cones or flower-spikes are terminal. Each sporophyll subtends only one sporangium, which springs from the stem above the leaf-axil. The same spike bears both macrosporangia and microsporangia. The macrosporangia (Fig. 354, *A-C*) are spherical, and each contains only four macrospores, which are produced by the growth and division of a single spore-mother-cell; all the other mother cells originally developed ultimately disappear. On account of the increasing size of the spores the macrosporangia become inflated and nodular. Opening occurs along definite lines of dehiscence, the wall splitting into two valves, which curve back from a boat-shaped basal portion. The spores are ejected by the pressure of the contracting boat-shaped part and the valves. Numerous spores are formed in the flattened microsporangia. The mode of dehiscence is similar in these also, but the boat-shaped portion of the wall is smaller, the valves extending to the base.

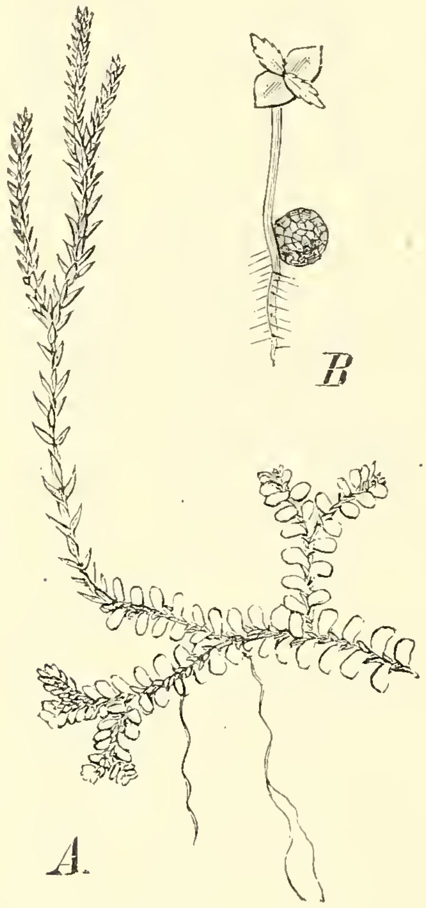


Fig. 353.—*A*, *Selaginella helvetica* (from nature, nat. size). *B*, *Selaginella denticulata*, embryonic plant with macrospore still attached. (After Bischoff, magnified.)

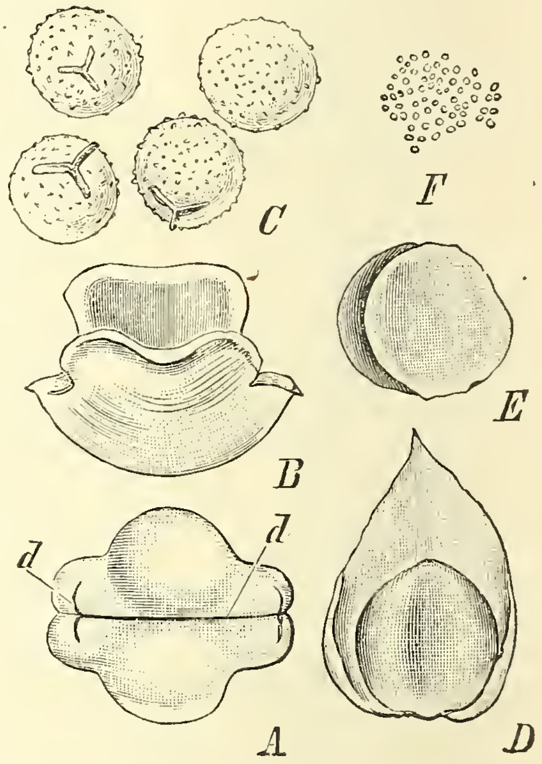


Fig. 354.—*Selaginella helvetica*. *A*, macrosporangium from above showing the line of dehiscence (*d*). *B*, opened, seen from the side; the four macrospores, *C*, have been ejected. *D*, microsporangium in the axil of its sporophyll. *E*, the same, opened. *F*, microspores. (× about 15.)

The microspores begin their development while still enclosed within the sporangium. The spore first divides into a small lenticular vegetative cell, which corresponds to the rhizoid cell of *Salvinia* (Fig. 346), and into a large cell, which divides successively into eight sterile peripheral cells and two or four central spermatogenous cells (Fig. 355, *A*). By the further division of the central cells numerous spermatozoid mother cells are formed (*B-D*). The peripheral cells then break down and give rise to a mucilaginous substance, in which is embedded the central mass of spermatozoid mother cells (*E*). The small prothallium-cell, however, persists. Eventually the wall ruptures, and the mother cells, thus liberated, set free the club-shaped biciliate spermatozoids (*F*). The reduction here exhibited in the formation of the male prothallium resembles that shown by the *Hydropterideae*.

The macrospores similarly begin their development within the sporangia.

After the division of the nucleus—which lies in the peripheral cytoplasm at the apex—into daughter nuclei and their distribution in the apical cytoplasm, the formation of cell walls begins. In this way, progressing from apex to base, the spore becomes filled by a process of multicellular formation, with large prothallium-cells. At the same time, and proceeding in the same direction, there begins a further division of these cells into smaller cells. In the tissue at the apex, consisting of small cells, the rudiments of a few archegonia appear, often even before the formation of the prothallium has been completed. The archegonia are usually not formed until the spores have been discharged from the sporangium.

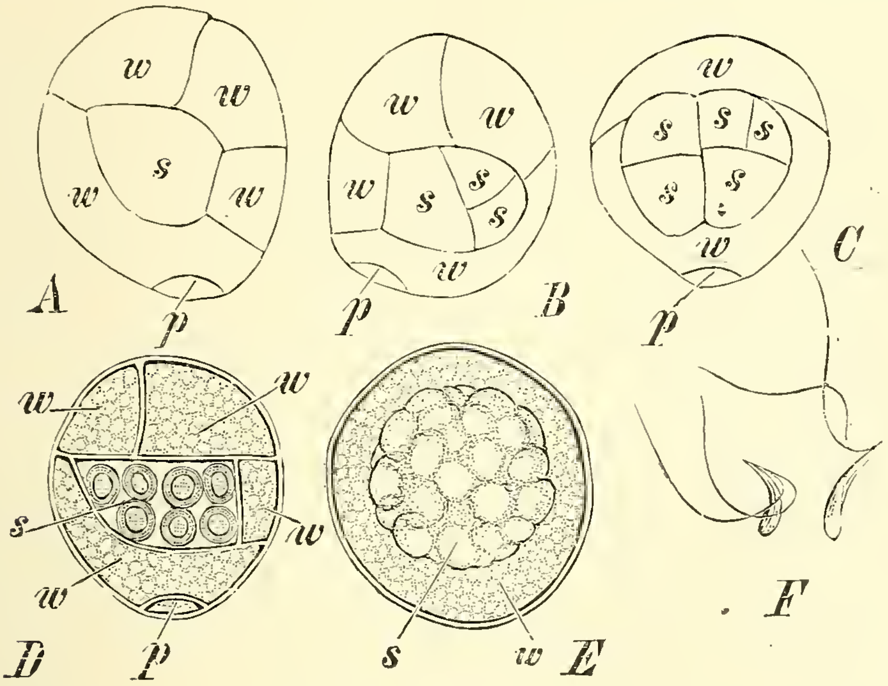


FIG. 355.—*A*-*E*, *Selaginella stolonifera*, successive stages in the germination of a microspore; *p*, prothallium-cell; *w*, wall-cells of antheridium; *s*, spermatogenous cells; *A*, *B*, *D*, lateral, *C*, dorsal view. In *E* the prothallium-cell is not visible, the disorganised wall-cells enclose the spermatozoid mother cells; *F*, spermatozoids of *Selaginella cuspidata*. (After BELAJEFF, *A*-*E* × 640, *F* × 780.)

The wall of the spore eventually bursts at the apex, and the prothallium becomes partially protruded. The fertilisation of one or two archegonia, which then takes place, is followed directly by the segmentation of the fertilised egg-cells in the formation of the embryos (Fig. 356).

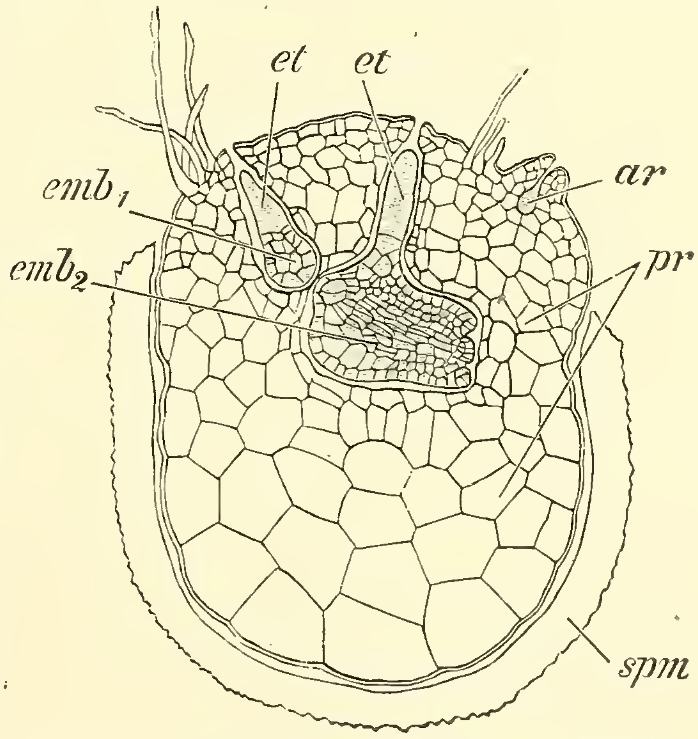


FIG. 356.—*Selaginella Martensii.* Female prothallium protruding from the apex of the ruptured macrospore; *spm*, wall of macrospore; *ar*, an unfertilised archegonium; emb$_1$, emb$_2$, two embryos, with suspensors *et*, sunk in the tissue of the prothallium. (After PFEFFER, modified, × 124.)

The embryogeny of *Selaginella* is very similar to that of *Lycopodium*. The egg-cell is divided by the formation of a transverse wall into two cells; the upper and larger cell increases considerably in size, and gives rise, by the division of its lower portion, to a suspensor (Fig. 357, *et*), while the lower cell, by repeated division, develops into an embryo, provided with two primary leaves and further segmented into stem, root, and foot (*bl*, *st*, *w*, *f*). The foot, in this instance, has another position and origin than in *Lycopodium.* Each primary leaf has, even at this stage, a ligule (*lig*) formed by the outgrowth of the leaf-base.

The suspensor is perpendicular to the axis of the embryo; its function is to push the embryo into the tissue of the prothallium, with which the foot, the organ of absorption, is thus kept in close contact. The stem apex, with the first pair of leaves, eventually grows upwards, and the root also extends beyond the macrospore. As the foot still remains in the prothallium the young plant continues united to the spore, and presents the appearance of a phanerogamic seedling with the seed still attached (Fig. 353, *B*).

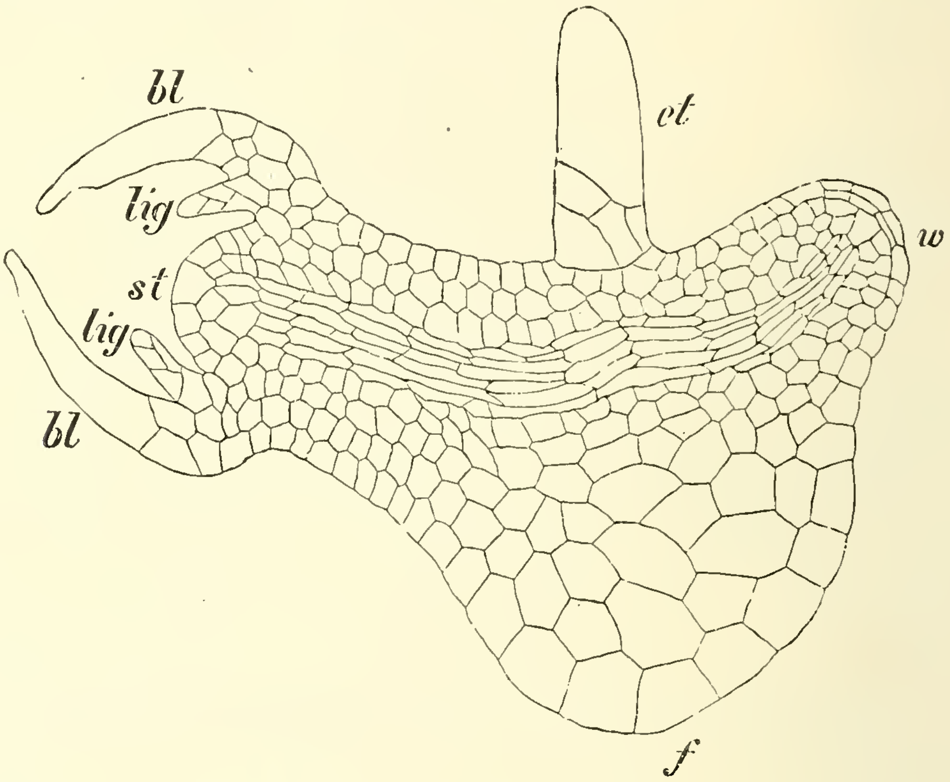


FIG. 357.—*Selaginella Martensii.* Longitudinal section of an embryo before its separation from the spore; *et*, suspensor; *w*, root; *f*, foot; *bl*, leaves; *lig*, ligules; *st*, apex of stem. (After PFEFFER, × 165.)

Order 3. Isoetaceae (75)

The isolated genus *Isoetes* must be regarded as a persistent branch of an ancient group of plants. It exhibits some affinities with the eusporangiate Ferns. The species of *Isoetes* are perennial plants, growing either on damp soil or submerged in water. The stem is short and tuberous, terminating below in a tuft of dichotomously branching roots, and above in a thick rosette of long, stiff, awl-shaped leaves (Fig. 358). The leaves are penetrated longitudinally by four air-passages, and expand at the base into a broad sheath. On the inner side of the leaves, above their point of insertion, is an elongated pit, the fovea, containing a large sessile sporangium. A ligule, in the form of a triangular membrane, is inserted above the fovea. *Isoetes* thus differs greatly in habit from the other genera, but resembles *Selaginella* in the development of a ligule.

The macrosporangia are situated on the outer leaves of the rosette; the microsporangia on the inner. Both are traversed by transverse plates of tissue or trabeculæ, and are in this way imperfectly divided into a series of chambers. The spores are set free by the decay of the sporangial walls.

The development of the sexual generation is accomplished in the same way as in *Selaginella*. The reduced male prothallium arises similarly within the spore, by the formation of a small, lenticular, vegetative cell, and a larger cell, the rudiment of a single antheridium. The larger cell divides further into four sterile peripheral cells, which completely enclose two central spermatogenous cells. From each of the latter arise, in turn, two spermatozoid mother cells, four in all, each of which, when liberated by the rupture of the spore wall, gives rise to a single, spirally coiled, multiciliate spermatozoid. The female prothallium, just as in *Selaginella*, also remains enclosed within the macrospore, and is incapable of independent growth. It shows similarly an approach to the Conifers, in that the nucleus first divides into numerous parietal daughter nuclei before the gradual formation of the cell walls, which takes place from the apex of the spore to the base. As a result of this process the whole spore becomes filled with a prothallium, at the apex of which the archegonia are developed. The embryo has no suspensor. In the structure of the embryo and of the spermatozoids *Isoetes* differs from the other *Lycopodineae*.

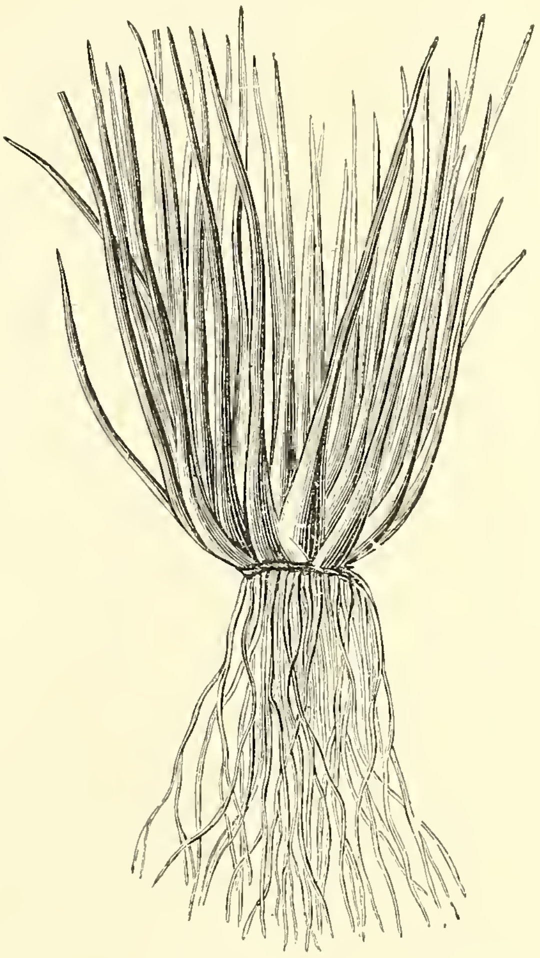


FIG. 358.—*Isoetes lacustris.* (½ nat. size.)

The Fossil Cryptogams (76)

The remains of cryptogamic plants of former geological periods afford no evidence as to the phylogenetic relations of the classes of Thallophyta and Bryophyta. Intermediate forms between Algæ and Bryophyta and between the latter group and the Pteridophyta are, as yet, unknown. On the other hand Phytopalæontology has made us acquainted with interesting long-extinct types of Pteridophytes which serve to complete the classification of the existing Ferns, Horse-tails, and Club-mosses, and in part afford a transition from the Ferns to the Gymnosperms.

The great majority of **Thallophytes** are, on account of their delicate structure, not adapted to be preserved in the fossil condition. The absence of remains of many classes of Thallophytes is therefore no ground for concluding that they did not exist in earlier periods. Even in the Silurian rocks remains of Algæ are found, though they do not permit of their relationship being determined. The remains of calcareous algæ belonging to the *Siphoneae* are, owing to their good preservation, among the best known; of these, forms are known from the Tertiary strata back to the Silurian, while the *Corallineae*, which are calcareous Red Seaweeds, appear from the Upper Jurassic onwards. Among unicellular Algæ the *Diatomaceae*, which have a silicified cell wall, are well preserved. The fossil forms frequently belong to existing genera, and occur from the Jurassic onwards, especially in the Cretaceous and Tertiary strata, often forming thick layers of Kieselguhr (diatomaceous earth). From Tertiary times onwards *Characeae* are abundant, and occasional remains are found as far back as the Muschelkalk. Most of the existing groups of Algæ are only to be distinguished with certainty from Tertiary strata onwards.

Bacteria must have played their part in causing the decomposition of organic substances from very early times; they can be distinguished in vegetable remains from Carboniferous rocks. The *Hyphomycetes*, and probably the *Myxomycetes* also, were present in Carboniferous times; *Ascomycetes* living on leaves and stems are found from the Carboniferous onwards in all strata. Remains of existing genera of Lichens appear in the Tertiary rocks.

II. **Bryophyta.**—Most of the examples of this group, which is rarely met with in the fossil condition, come from the Tertiary strata and resemble existing genera closely. Only isolated examples of Liverworts and Mosses occur in the older rocks (Jurassic, Upper Triassic).

III. The **Pteridophyta** extend back to Silurian times, but were most highly developed in the Carboniferous period, when they formed the main mass of the land vegetation. With the advent of Gymnosperms, and later of Angiosperms, their relative importance in this respect diminished.

1. The class of **Filicinae** was represented by forms belonging to the true Ferns or *Filices* at the end of the Silurian period, and large numbers of species occur in the Carboniferous strata. The organisation of these ancient types was essentially similar to that of the existing forms. Most of the recent families were represented, some (*e.g. Marattiaceae*) more fully than at the present time. The *Cycadofilices*, fern-like plants with secondary thickening, only the vegetative organs of which are as yet known, appear to have given rise to the Phanerogams, or at least to the *Cycadaceae*. The other classes of Pteridophyta do not appear to have given origin to higher forms.

The *Hydropterideae* are known with certainty from the Tertiary rocks, but *Salvinia* and *Marsilia* can be traced back to the Chalk.

2. The class of the **Equisetineae** represented at present by the single genus *Equisetum*, which can be traced back to the Triassic period, was much better developed in Palæozoic times. The large order *Calamarieae* consisted of plants resembling the Horse-tails in general habit, but in some cases attaining the size of trees 30 metres high; the hollow stem bore whorls of branches at the nodes, was covered with a periderm, and underwent secondary thickening. The leaves (*Annularia*) stood in alternating whorls; their form was narrowly lanceolate and at their bases they united into a sheath. In the most ancient type, *Archaeocalamites*, they were dichotomously divided. The cones or flowers (*Calamostachys*) had in some the same structure as those of *Equisetum;* in most cases they were more complicated, whorls of scale-leaves alternating with the sporophylls. At least some of the *Calamarieae* were heterosporous.

3. The **Lycopodinae** were also abundantly represented in Palæozoic times, especially by the two great extinct orders, the *Sigillarieae* and the *Lepidodendreae.* The *Sigillarieae*, found from the Culm onwards, are most numerous in the Carboniferous period, and persist with one species in the Bunter Sandstone. They were stately trees, with but little branched pillar-like stems, which grew in thickness. They had long narrow leaves, which when they fell off left longitudinal rows of hexagonal leaf-scars on the surface of the stem. Long-stalked, cone-like flowers originated from the stem; only one kind of spore was contained in the sporangia.

The *Lepidodendreae* extend from the Lower Devonian to the Rothliegende, but are also best developed in the Carboniferous period. They were tree-like plants with dichotomously branched stems which grew in thickness. The leaves, which attained a length of 15 cm., were spirally arranged and seated on rhombic leaf-cushions. The cone-like flowers (*Lepidostrobus*) were borne on the ends of branches or sprang from the stem itself; each sporophyll bore a single sporangium, which contained either macrospores or microspores.

Smaller *Lycopodiaceae* the predecessors of the existing species of *Lycopodium*, were already present in the Carboniferous flora, while *Isoetes* is only known with certainty from the lower Cretaceous strata.

IV. The small class of the **Sphenophyllinae**, which existed from the Devonian to the Permian and then died out, possesses special morphological interest since it occupies an intermediate position between *Lycopodinae* and *Equisetinae*. Possibly it is the least altered from the common ancestral form of these three groups. This especially holds for the most ancient type *Cheirostrobus*, which occurs in the Lower Carboniferous rocks. The cones of this genus had a very complicated structure, reminding one of the calamarian cone, while the anatomy exhibits an approximation to the type of *Lepidodendron*.

The species of *Sphenophyllum* were plants with elongated stems, bearing superposed whorls of triangular or more or less dichotomously-divided leaves. The cones were large and terminal, resembling those of *Equisetum*; each sporophyll bore two or three homosporous sporangia. These plants have been regarded as aquatic, but the structure of the elongated thin stem, with a triangular mass of primary xylem and subsequent secondary thickening, rather suggests that they were climbing plants which grew on land.

PART II

SPECIAL BOTANY

SECTION II

PHANEROGAMIA

SECTION II

PHANEROGAMIA (1, 2)

ALTHOUGH it has long been customary to place the Phanerogams in contrast to the Cryptogams as the two main divisions of the vegetable kingdom, it must be admitted that the boundary between them is less clearly defined than those between the various groups of Cryptogams. THE MOST ANCIENT TYPES OF THE PHANEROGAMS CORRESPOND CLOSELY TO THE HETEROSPOROUS PTERIDOPHYTES; the alternation of generations is the same, and there is an essential agreement in both vegetative and reproductive parts in the two groups. Differences are exhibited, not in main characters, but in a number of secondary points which have attained more and more importance during the phylogenetic development, and, taken together, characterise the Phanerogams as the most highly developed plants.

The reason that the names of the various members of the organism differ in the Phanerogams and the Pteridophyta is that they were applied at a time in which the homologies between the two groups were not known. It is owing to the work of W. HOFMEISTER (3) that these relations were made clear about the middle of the last century. Unfortunately the older terms are strongly rooted and the male sporophylls of Phanerogams are still termed STAMENS, the microsporangia POLLEN-SACS, the microspores POLLEN-GRAINS, and the portion of the stamen which bears the pollen-sacs, if it is specially differentiated, the ANTHER. The female sporophylls are the CARPELS, the macrosporangia OVULES, the macrospore the EMBRYO-SAC.

The POLLEN-GRAINS (4) are, like the microspores of Pteridophytes, produced in large numbers in the pollen-sacs. The development of the pollen-sacs and pollen-grains (Fig. 359) is effected in the same way as the homologous reproductive organs of the Pteridophytes. A cell layer, directly under the epidermis of the sporophylls, becomes divided by tangential walls into two layers, the outer of which contributes to form the wall of the sporangium, the inner the sporogenous tissue. The latter, by repeated division, give rise to the pollen mother cells, each of which divides into four pollen-grains (Fig. 359). Although the pollen-grains sometimes remain united in tetrads (Fig. 360, *A*), they are generally isolated, and have the appearance of round or elongated bodies, which are at first unicellular (Figs. 360 *B*, 361), but eventually, in consequence of the formation of a reduced male prothallium, become multicellular.

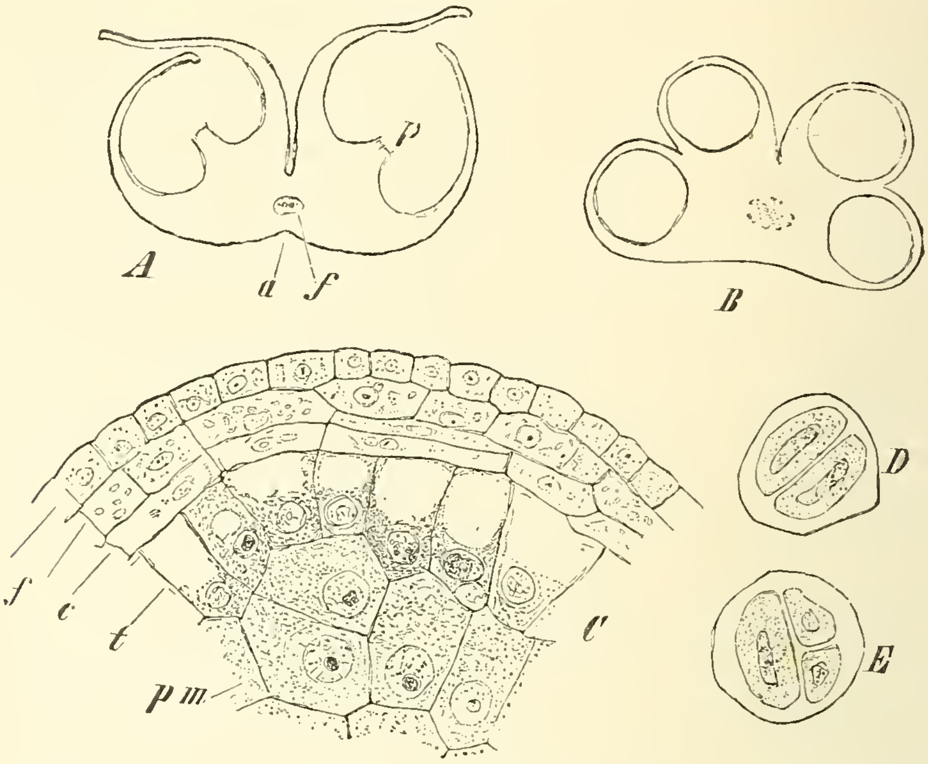


FIG. 359.—*Hemerocallis fulva.* *A*, Transverse section of an almost ripe anther, showing the loculi ruptured in cutting ; *p*, partition wall between the loculi ; *a*, groove in connective ; *f*, vascular bundle (× 14) : *B*, transverse section of young anther (× 28) : *C*, part of transverse section of a pollen-sac ; *pm*, pollen mother cells ; *t*, tapetal layer, later undergoing dissolution ; *c*, intermediate parietal layer, becoming ultimately compressed and disorganised ; *f*, parietal layer of eventually fibrous cells ; *e*, epidermis (× 240) : *D* and *E*, pollen mother cells after division (× 240).

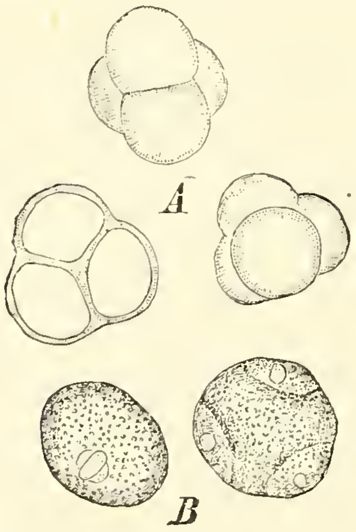


FIG. 360.—*A*, Pollen-grains of the Heather (*Calluna vulgaris*), cohering in tetrads ; *B*, simple pollen-grains of the Lime (*Tilia*). (× 350).

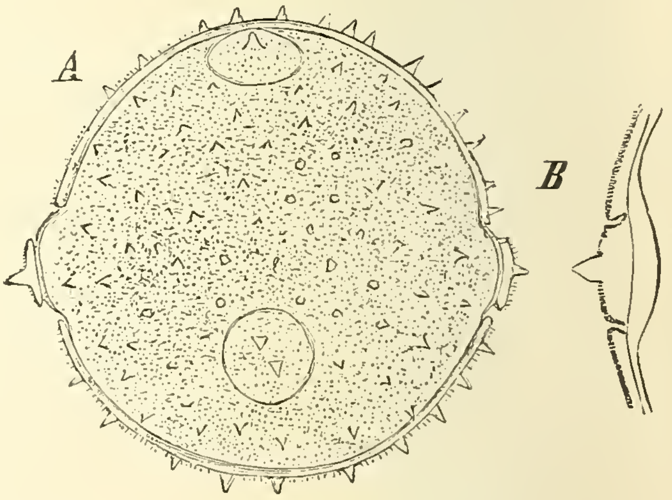


FIG. 361.—*A*, Pollen-grain of *Cucurbita Pepo* (× 240) ; *B*, section of pollen-grain of *Cucurbita verrucosa*, showing one of the lid-like areas through which the pollen-tubes protrude (× 540).

Each pollen-grain is provided with a delicate wall, which is differentiated into a cuticularised EXINE, and an INTINE consisting chiefly of pectose. The surface of the pollen-grain is frequently studded with projecting points or warts, or beset with delicate and regularly disposed outgrowths. In addition, thinner spots (Fig. 361, *A*) or areas defined by a lid-like covering (Fig. 361, *B*) often occur in the walls of the pollen-grains; they fulfil an important office as GERM-PORES in facilitating the processes of fertilisation.

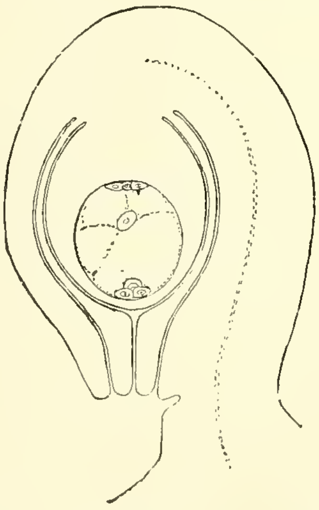


Fig. 362.—Longitudinal section of the ovule of *Narcissus poeticus* (after A. Meyer).

An ovule (^{5}) (Fig. 362), when ready for fertilisation, is represented by an ellipsoidal body attached to the carpel, usually by a stalk, the FUNICULUS. The central portion of the ovule is occupied by a club-shaped mass of tissue termed the NUCELLUS. Enveloping the nucellus are one or two sheathing coats, the INTEGUMENTS, which spring from its basal portion, the so-called CHALAZA. The integuments are prolonged beyond the nucellus as a short neck traversed by a canal known as the MICROPYLE.

Sometimes the axis of the ovules forms a continuous line with the funiculus, the ovule is then straight (Fig. 363, *A*), and is said to be ATROPOUS (orthotropous). If the funiculus curves sharply, immediately below the ovule, so that both lie side by side, the ovule is inverted or ANATROPOUS (Figs. 362, 363 *B*). In this, the most frequent case, the funiculus is in part adherent to the outer integument, and forms a suture or RAPHE on the seed along the line of contact. Less frequently the ovule is CAMPYLOTROPOUS (Fig. 363, *C*), and is itself so curved that the chalaza and micropyle do not lie in the same straight line.

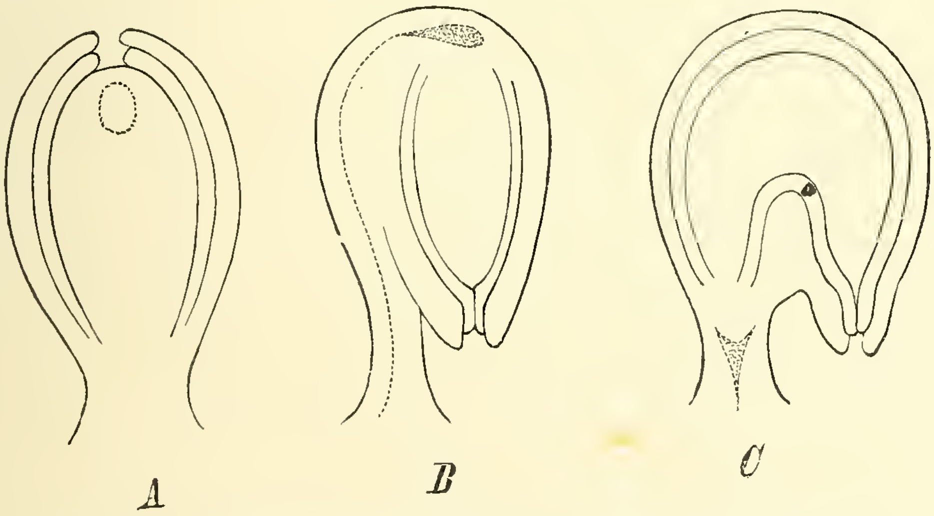


Fig. 363.—*A*, Atropous; *B*, anatropous; *C*, campylotropous ovules. (Diagrammatic and magnified.)

As a rule, only one macrospore, the so-called EMBRYO-SAC, is formed in each nucellus. UNLIKE THE MACROSPORE OF THE PTERIDO-

PHYTES, THE EMBRYO-SAC ALWAYS REMAINS ENCLOSED IN THE MACROSPORANGIUM, AND IS ORGANICALLY UNITED WITH IT. In a few cases several embryo-sacs are produced in the same nucellus.

The comparison of the spore-bearing generation of the most primitive Phanerogams with that of the Pteridophyta shows that in spite of the great similarity a higher grade of development is attained by the former.

The Phanerogams, which stand nearest to the Pteridophytes, constitute the sub-class *Gymnospermae*. They must be regarded on account of their morphological characters as the most primitive phanerogamic plants. Their occurrence in the oldest formations, such as the Devonian, while the Angiosperms first appear in the Cretaceous period, further supports this.

The Gymnosperms of the Devonian, and most of those of the Carboniferous and Permian periods, while showing many points of connection with existing forms, belong to types which have become extinct. The distinction between Pteridophytes and Gymnosperms was even less marked than it now is. Many forms, the vegetative organs of which are as yet only known, combined the peculiarities of the two classes. These forms, the structure of which is known very thoroughly, are grouped as *Cycadofilices*. The extinct genus *Cordaites*, the reproductive organs of which are known, shows considerable indications of a simpler type. THE STRUCTURAL CHARACTERS OF THE PRIMITIVE GYMNOSPERMS WHICH ARE NOW EXTINCT INDICATES THE FILICINAE AS MOST NEARLY RELATED TO PHANEROGAMS; THE RESEMBLANCES BETWEEN THE LATTER AND THE LYCOPODINAE DEPEND ON ANALOGY. In the absence of any knowledge of the reproductive organs of the *Cycadofilices* it is useless to speculate on the relationship of the Gymnosperms to particular groups of Pteridophyta, *e.g.* as to the relationship between the *Marattiaceae*, which were so abundant in Palæozoic times, and the *Cycadaceae*, the habit of which is so similar.

THE PROGRESS WHICH IS EVIDENT ON COMPARING THE MOST PERFECT PHANEROGAMIC TYPE WITH THAT OF THE FERNS IS CONFINED TO THE SPOROPHYTE, WHICH OBTAINS A MORE AND MORE COMPLETE EXTERNAL AND INTERNAL DIFFERENTIATION; THE SEXUAL GENERATION, ON THE OTHER HAND, BECOMES MORE AND MORE REDUCED. While in the Gymnosperms this generation stands at about the same level as in the *Hydropterideae*, the Angiosperms only show feeble traces of it.

The more complete organisation of the shoot in Phanerogams is most marked in the reproductive portions. In the vegetative regions the advance is confined to more perfect histological differentiation, while the sporophylls and neighbouring organs, in the higher Phanerogams at least, show a special external form. While great variety is found in the individual cases, the form of these organs is in all cases closely connected with the process of fertilisation, and is to be regarded as adapted in relation to it.

Structure of the Flower (6).—The sporophylls of Phanerogams are always aggregated in groups; a special shoot, or the apical region of a shoot which is vegetative below, forms the fertile shoot bearing sporophylls only, or, in the higher Phanerogams, a PERIANTH surrounding these. In most cases both kinds of sporophylls are present, the stamens surrounding the centrally placed carpels. In addition to such hermaphrodite flowers, unisexual ones occur. Both kinds of unisexual flowers may be borne on the same plant (MONŒCIOUS), or they may occur on separate plants (DIŒCIOUS). In most cases unisexual flowers characterise the lower forms; they are thus the rule in Gymnosperms. Where they make their appearance in higher forms they have originated by reduction from hermaphrodite flowers, and often exhibit rudiments of the organs which have been lost.

From the constant occurrence of flowers, it is often customary to refer to the Phanerogams as the FLOWERING PLANTS. It must not, however, be concluded that this is characteristic of the Phanerogams alone, for the aggregated sporophylls of the cones of the *Equisetaceae* or of the spikes of the *Lycopodiaceae* are true flowers standing on the same grade of development as those of the Gymnosperms. An instance of the first step towards the formation of a flower is shown by the existing Fern *Blechnum*. The sporophylls are differently constructed in the more ancient group of Gymnosperms and in the Angiosperms which have arisen later in the course of phylogenetic development. In the former they resemble closely the fertile leaves of some *Pteridophyta*, being scale-like structures arranged in a close spiral around a long thin axis. The perianth is wanting or indicated by a few scale-leaves. The number and arrangement of the pollen-sacs on the stamens differs in the several subdivisions; the number of ovules also varies. The ovules are naked, being situated on the margins of carpels which never become united to form a closed cavity.

In the Angiosperms the floral axis is nearly always short and thick, and usually more or less dilated above. The floral leaves are with few exceptions arranged in whorls. In some apparently primitive Angiosperms the perianth is wanting, or is small and inconspicuous: in the more highly developed forms it has become the largest and most prominent part of the flower. This change stands in relation to the introduction of a new factor into the phylogenetic development. While in Gymnosperms and the more primitive Angiosperms the agencies of wind and water serve to convey the pollen to the ovules, in the later forms this is effected by the agency of insects. This conducts the formative forces of the flower into new channels and results in numerous wonderful adaptations. The endless variety in form of the Angiospermic flower, the various colouring, the scent, and the secretion of nectar are all adaptations to pollination by insects. In some regions (Tropics, South Africa) birds also effect the same end.

The perianth (Fig. 364) tends to be formed of two whorls, an external, green, protective layer, the Calyx, and an inner, more conspicuous and delicate whorl, the Corolla. The former approaches the foliage leaves in structure, the latter is not green in colour and serves the purpose of attracting the pollinating insects. When the leaves of the perianth are all similar or when only one series is present it is termed the PERIGONE; the perigone may be sepaloid or petaloid.

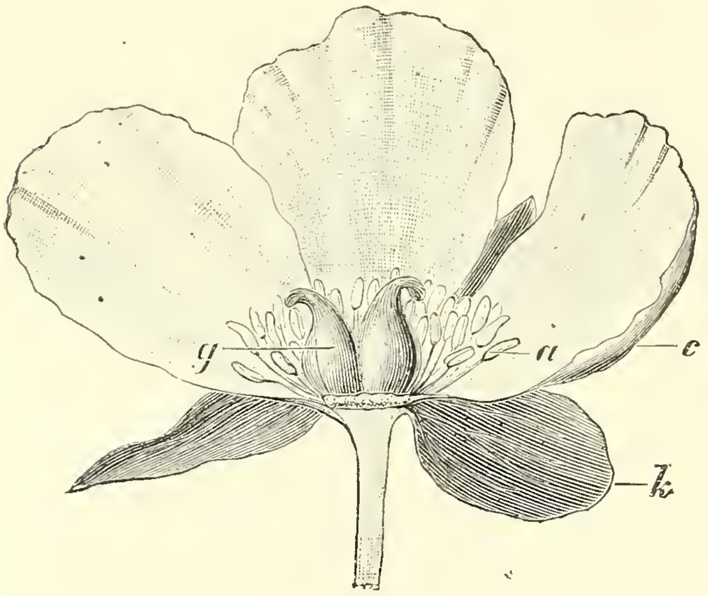


Fig. 364.—Flower of *Paeonia peregrina*, in longitudinal section. *k* and *c*, Perianth; *a*, andrœcium; *g*, gynœcium. (Nat. size.)

In hermaphrodite and male flowers the whorl of stamens which, taken together, constitute the Andrœcium, succeeds the perianth and alternates with it. The carpels, which in hermaphrodite flowers follow the stamens and in female flowers come immediately above the perianth, are termed collectively the GYNŒCIUM.

In the Angiosperms the stamens are filiform and are divided into the FILAMENT and the ANTHER (Fig. 366). The former serves simply to bear the latter, which as a rule consists of two THECÆ and the CONNECTIVE between them; each theca contains two pollen-sacs. According to the position of the theca on the ventral or dorsal side of the anther the latter is termed introrse or extrorse. Each theca usually opens by a longitudinal slit, so situated along the partition walls between the two pollen-sacs that it is common to both (Fig. 359, *A*). Other modes of dehiscence will be found mentioned in the special part.

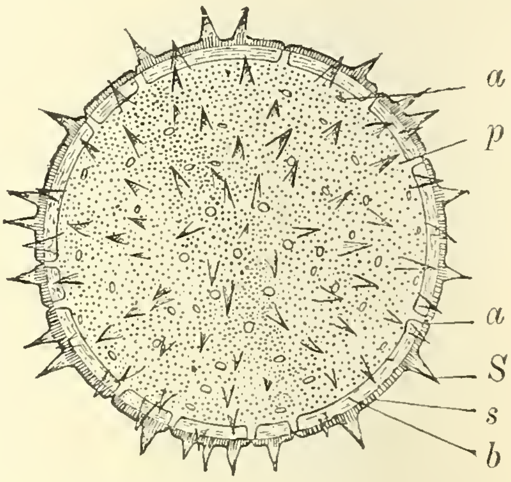


Fig. 365.—Pollen-grain of *Malva silvestris*. *S*, Spinous projections of the exine; *s*, vertically striated layer of the exine; *p*, the same seen from above; *a*, places of exit of pollen-tubes. (After A. Meyer.)

The pollen differs in anemophilous and entomophilous flowers. In the former it is dry, so that it is easily dislodged from the anthers and carried away by movements of the air; the individual grains are small and their surface smooth. The pollen of flowers which are pollinated by insects or birds, on the other hand, is sticky and remains attached to the anthers; it becomes attached to the bodies of the animal visitors by reason of the rapid drying of its surface, and in many cases by spines and other outgrowths (Fig. 365).

The stamens, although generally quite free from each other, are sometimes coherent into several bundles, as in *Hypericum;* or, as in *Ononis*, into a tube, or into a column, as in the case of *Cucurbita*. The cohesion may extend throughout their whole length (*e.g. Cucurbita*), or it may be restricted to the filaments.

By the branching of the stamens an appearance is produced similar to that resulting from their fusion. It is often only possible to determine which may be the case by a comparative study of their mode of development in allied forms. Sometimes the branched character of the stamens is indicated by the fact that the anthers each contain only one theca, and appear to be halved. Undoubted examples of branching are afforded, for instance, by the flowers of *Ricinus*, with tree-like, branching stamens, or by those of the *Malvaceae*, in which the stamens are coherent below and branched above (Fig. 367).

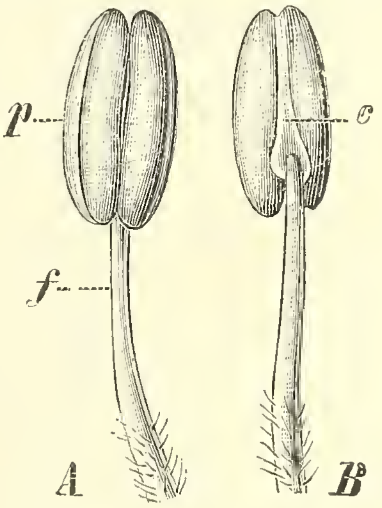


FIG. 366.—*A* and *B*, anterior and posterior view of a stamen of *Hyoscyamus niger*; *f*, the filament; *p*, anther; *c*, connective (magnified).

The andrœcium springs directly from the floral axis, or it is adnate to other portions of the flower, in particular to the perianth.

The term STAMINODES is applied to sterile stamens which perform at most only a secondary function in the process of fertilisation.

Great weight was formerly attached by systematists to the mode of insertion of the andrœcium. It was then customary to distinguish *Thalamiflorae*, *Corolliflorae*, or *Calyciflorae*, according as the stamens were inserted on the receptacle, the corolla, or the calyx. *Calyciflorae*, as a matter of fact, do not occur, as in such cases the supposed calyx is in reality the expanded floral axis.

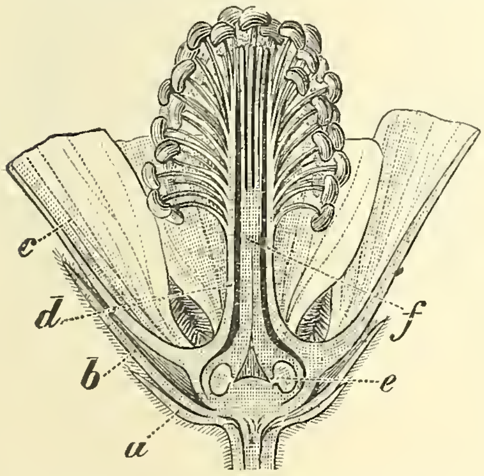


FIG. 367.—*Althaea officinalis*, flower cut through longitudinally; *a*, epicalyx; *b*, calyx; *c*, corolla; *d*, andrœcium. (After BERG and SCHMIDT, magnified.)

The GYNŒCIUM is always the terminal structure of the flower, occupying the apex of the floral axis. It is either composed of separate members, APOCARPOUS (Fig. 368, *A*), or the members are united, SYNCARPOUS (*B*, *C*). In the first case the margins of each carpel are so joined together that each forms a distinct OVARY or closed cavity containing the ovules. The carpels of a syncarpous gynœcium, on the other hand, are coherent and form collectively a single ovary, which may be either plurilocular when the coherent margins of the carpels extend to the axis, or unilocular if the carpels cohere simply by their edges, and do not turn inward, or only slightly.

The double walls or DISSEPIMENTS of a plurilocular ovary, formed by the inwardly projecting margins of the coherent carpels, are distinguished as TRUE, in contrast to the FALSE DISSEPIMENTS which, in rare cases (*e.g. Labiatae*), are produced by ingrowths from the internal surface of the carpels.

The ovary is prolonged upwards as a neck-like STYLE, expanded at the apex into a STIGMA, which may be of various shapes. The whole organ, consisting of ovary, style, and stigma, is termed the PISTIL.

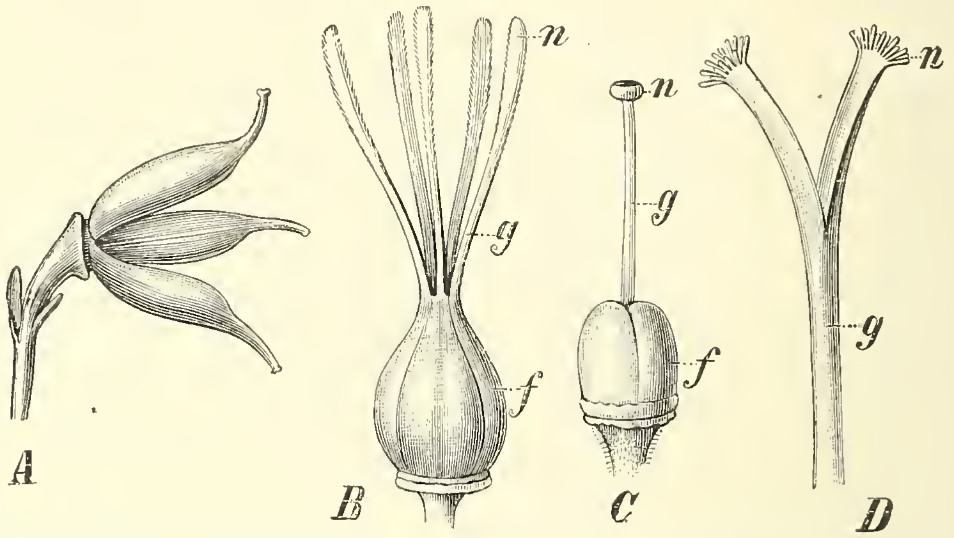


FIG. 368.—Different forms of gynœcia. *A*, Of *Aconitum Napellus; B*, of *Linum usitatissimum; C*, of *Nicotiana rustica; D*, style and stigma of *Achillea Millefolium; f*, ovary; *g*, style; *n*, stigma. (After BERG and SCHMIDT, magnified.)

A completely syncarpous gynœcium possesses but one ovary and one stigma (Fig. 368, *C*). The cohesion of the carpels may, however, be restricted to the basal portions in such a way that the ovary bears as many separate styles, or a style as many stigmas, as the number of carpels united in the ovary (*B*, *D*). The reverse case, in which only the upper portions of the carpels cohere, and not the lower, occurs only in the *Apocynaceae* and *Asclepiadaceae*.

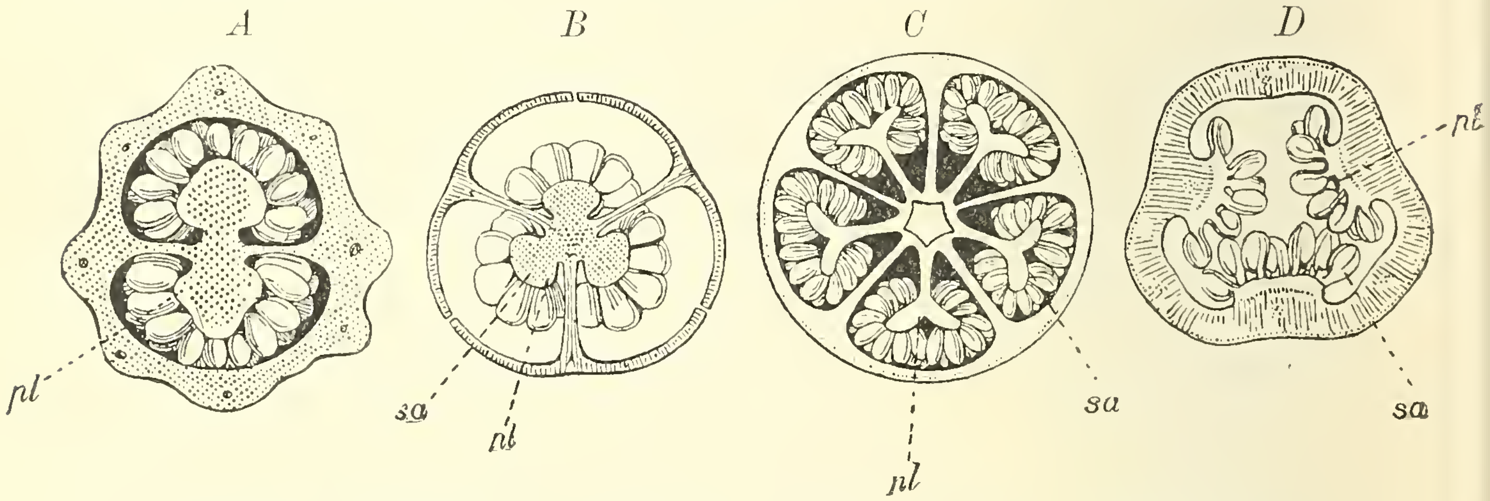


FIG. 369.—Transverse sections of ovaries. *A*, *Lobelia; B*, *Diapensia; C*, *Rhododendron; D*, *Passiflora; pl*, placenta; *sa*, ovules. (After LE MAOUT and DECAISNE.)

The style exhibits great variation in length and thickness. It is, for example, long and filiform in *Crocus*, short and thick in *Tulipa*. It is either traversed by an axial canal or filled with a loose parenchyma.

The stigma may be disc-shaped, ellipsoidal, capitate, bifurcate, or more rarely, as in *Iris*, corollaceous. Its surface is generally velvet-like, covered with papillæ, and is moist and sticky.

The ovules are always enclosed in the cavity of the ovary. They are developed, as a rule, from the margin of the carpels, and are therefore in unilocular ovaries parietal (Fig. 369, *D*); in plurilocular, axile or axillary (*B*).

Sometimes a departure from this mode of development of the ovules is exhibited, and the placentation instead of being marginal is superficial; the ovules are distributed, as in *Butomus*, over the whole inner surface of the carpels. In other cases, again, the placentation is free-central and the ovules appear to be produced from the floral axis itself, as in the orders *Centrospermae*, *Polygoninae*, and *Primulinae* (Fig. 370). In the last case, the anomalous position of the ovules is attributed to the disappearance of the dissepiments, or to their coalescence and displacement. The portion of the wall of the ovary, from which the ovules arise, usually projects more or less into the cavity; it is termed a PLACENTA (Fig. 369, *pl*).

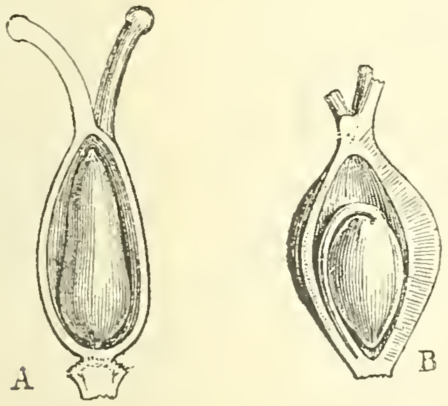


FIG. 370.—Ovaries containing basal ovules. A, *Fagopyrum esculentum* (atropous); B, *Armeria maritima* (anatropous) shown in longitudinal section. (After DUCHARTRE. × 20.)

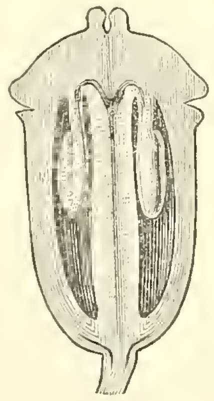


FIG. 371.—Ovary of *Foeniculum officinale* with pendulous ovules, in longitudinal section. (After BERG and SCHMIDT, magnified.)

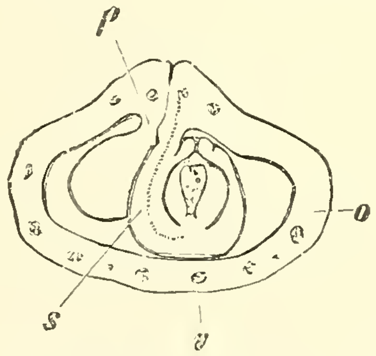


FIG. 372.—Transverse section of an ovary of *Delphinium Ajacis*, showing ovule placed horizontally; *s*, ovule; *p*, placenta; *o*, wall of ovary; *v*, vascular bundles. (× 18.)

The position assumed by the ovules themselves in the cavity of the ovary may be ERECT (*e.g. Fagopyrum*, *Armeria*, Fig. 370), HANGING (*e.g. Umbelliferae*, Fig. 371), or HORIZONTAL (*e.g. Delphinium*, Fig. 372). The raphe is VENTRAL when it is turned towards the placenta, DORSAL when turned away from it.

The FLOWER-AXIS (RECEPTACLE, TORUS) is usually thicker than the flower-stalk, of which it occupies the apex. It frequently expands by intercalary growth between the andrœcium and gynœcium, into a disc, cupular, or urn-shaped body, which affects essentially the general appearance of the flower. In the simplest cases the flower-axis is club-shaped, and the floral whorls succeed each other in tiers. Such flowers are said to be inferior or HYPOGYNOUS; their ovaries, SUPERIOR (Figs. 373 *A*, 374). When the axis is developed as a concave receptacle, so that the gynœcium is inserted at the same height as the andrœcium or lower, but free and not coalescing with the axis, the flower is PERIGYNOUS, the ovary HALF-INFERIOR (Figs. 373 *B B′*, 375 1, 2); but if the ovary is adherent to the axis, it is described as INFERIOR; the flower as superior or EPIGYNOUS (Figs. 373 *C*, 375 3). Only the

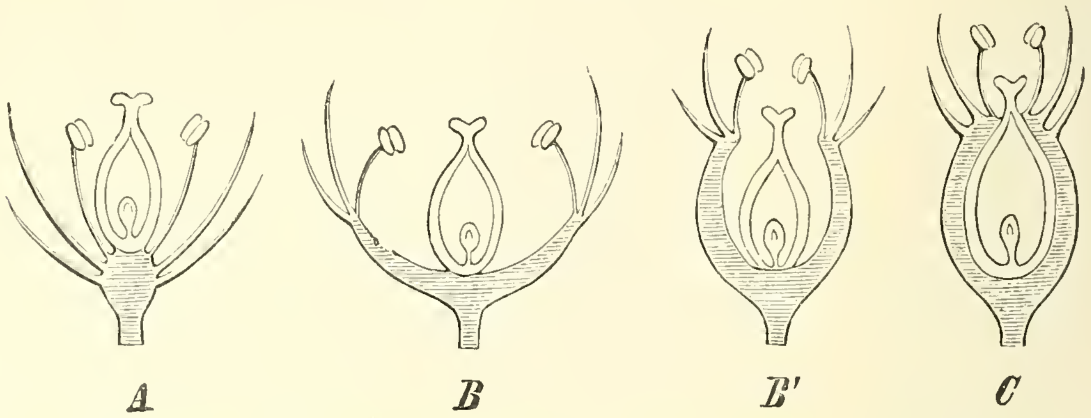


FIG. 373.—Diagrams of (*A*) hypogynous (*B*, *B′*), perigynous, and (*C*) epigynous flowers.

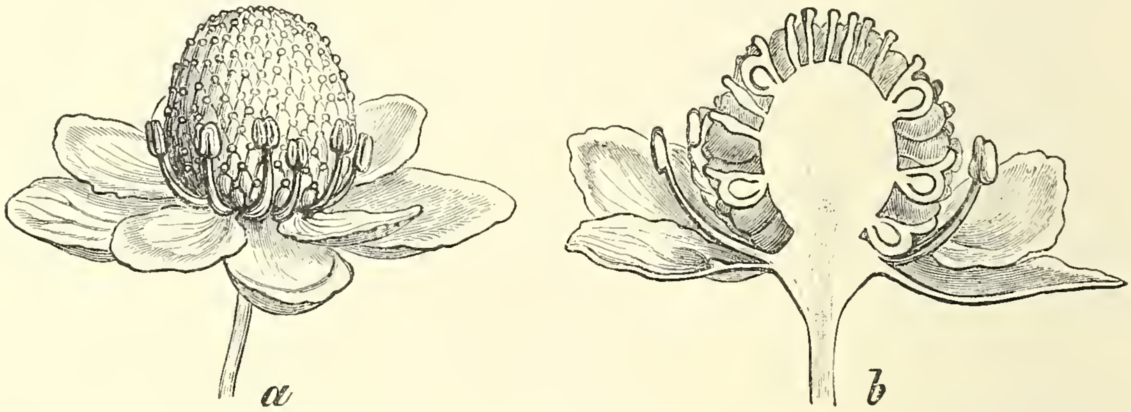


FIG. 374.—Hypogynous flower of *Ranunculus sceleratus* with numerous, superior ovaries borne upon a club-shaped receptacle. (After BAILLON, magnified.)

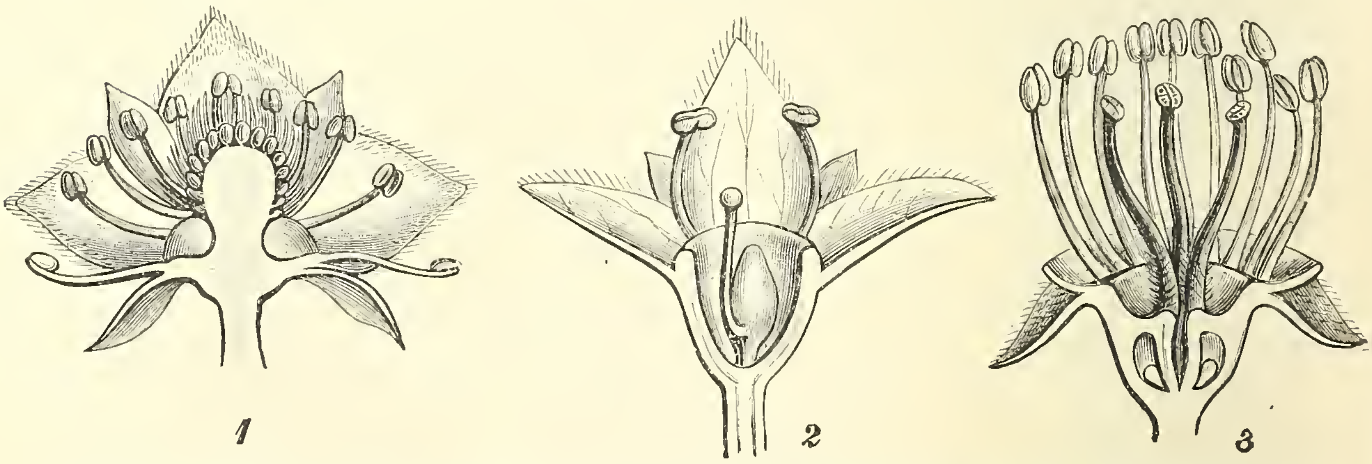


FIG. 375.—Different flowers belonging to the family *Rosaceae*, cut through longitudinally. 1, *Potentilla palustris*, hypogynous; 2, *Alchemilla alpina*, perigynous; 3, *Pirus Malus*, epigynous. (After FOCKE in *Nat. Pflanzenfamilien*, magnified.)

internal portion of an inferior ovary formed by the carpels is accordingly homologous, with a superior or half-inferior ovary. Transitional forms between these different modes of insertion of the ovary frequently occur ; thus a flower may be slightly perigynous (many *Leguminosae*) or imperfectly epigynous.

The flower-axis can, in addition, by the formation of outgrowths of different natures, essentially modify the structure of the flower. These accessory structures are sometimes large and corollaceous, as in *Passiflora*, but they are usually inconspicuous and confined to the DISC. The latter constitutes either a continuous ring or a circle of glands or scales, occupying generally a position between the androecium and gynœcium (Fig. 376). The disc usually secretes a sweetish fluid, and is then termed a NECTARY, in consequence of its biological function. Other parts of the flower, the petals for instance, may be developed as nectaries (*Aconitum*).

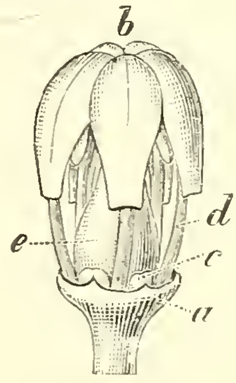


FIG. 376.—Flower of *Vitis vinifera*. *a*, Calyx; *b*, corolla ; *c*, disc-glands between the stamens *d* : *e*, gynœcium. (After BERG and SCHMIDT, magnified.)

Arrangement and Number of the Floral Leaves (7).—In some Angiosperms, as in most Gymnosperms, the floral leaves are all or in part arranged spirally. Flowers in which the spiral arrangement of the leaves prevails, as, for example, is generally the case in the *Ranunculaceae*, are termed ACYCLIC.

In a large majority of Angiosperms the flowers are CYCLIC, and have their leaves arranged in whorls. Most frequently five successive whorls are present, alternating regularly with each other. Of these, two belong to the perianth, two to the androecium, and one to the gynœcium. Flowers constructed after this type are described as PENTACYCLIC (Fig. 377).

The number of parts in a whorl is usually the same in the perianth and androecium—in Monocotyledons generally three, in Dicotyledons five. This uniformity in the number of members in the whorls may also extend to the gynœcium ; but, as a rule, particularly in Dicotyledons, the number of carpels is smaller. The number of members in the whorls of the perianth, androecium, and gynœcium is indicated by the terms di, tri, tetra, pentamerous, etc.

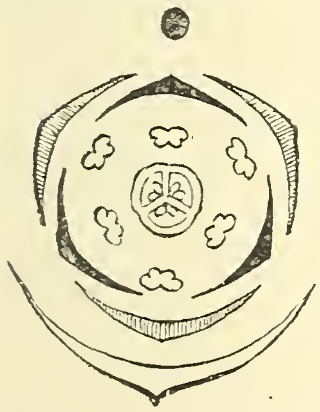


FIG. 377.—Diagram of a pentacyclic flower (*Lilium*).

A TYPICAL ANGIOSPERMOUS FLOWER IS CONSTRUCTED OF FIVE ALTERNATING ISOMEROUS WHORLS, OF WHICH TWO BELONG TO THE PERIANTH, TWO TO THE ANDRŒCIUM, AND ONE TO THE GYNŒCIUM. Flowers varying from this type have either continued in an undeveloped stage, as those of the amentaceous plants, or, like the acyclic flowers, they belong to a family which has been separated from the main line of descent, or they have been subsequently modified from the normal type in the course of phylogenetic evolution, like the flowers of the *Orchidaceae* and *Labiatae*.

Only such variations from typical Angiosperm flowers are mentioned in this general summary as may have arisen by subsequent modification. To avoid repetition the other special cases will be considered later in the detailed description of the single flowers.

A simple and not infrequent variation from the normal structure is presented in flowers in which the stamens of the outer whorl are opposite the petals, and those of the inner whorl opposite the sepals. An andrœcium of this character is termed OBDIPLOSTEMONOUS, as distinct from the typical DIPLOSTEMONOUS arrangement of the stamens.

Another of the more common variations from the original type is due to the MULTIPLICATION OF THE WHORLS, often occurring in the andrœcium (Rose), less frequently in the perianth (*Berberis*), very rarely in the gynœcium (*Punica Granatum*).

A variation of even more frequent occurrence results from the DIMINUTION OF THE NUMBER OF WHORLS. This is often shown in unisexual flowers, although by no means in all cases, as the missing organs may be represented by reduced and functionless parts, as in the similar case of the mammary glands of male mammals. Thus in the female flowers the place of the stamens is not uncommonly occupied by sterile staminodia. In hermaphrodite flowers also a reduction of the number of whorls is often shown. The occurrence of flowers with a simple perianth has already been mentioned; flowers with a simple andrœcium are still commoner.

Such examples cannot, in all cases, be attributed to a reduction from the normal pentacyclic type. On the contrary, they often represent a primitive, more simple type (*e.g.* the flowers of the Nettle and its allies). The absence of a whorl may only be referred to its suppression, when such a conclusion is corroborated by other evidence, such as, for example, may be derived from a comparison of allied forms, as in the case of the *Orchidaceae*, in which the andrœcium is represented sometimes by an outer, sometimes by an inner whorl, while the perianth and gynœcium at the same time exhibit the highest stage of development.

Flowers in which the andrœcium is formed by a single complete whorl are said to be HAPLOSTEMONOUS.

In addition to the number of the whorls, the number of the members composing the single whorls is subject to variation, and is due similarly, in many if not in all cases, to their subsequent diminution by reduction or to their multiplication by splitting.

A decrease in the number of the floral leaves of a single whorl is most frequently met with in the gynœcium, which, in flowers with a pentamerous perianth and andrœcium, has usually but three or even two carpels. Next to the gynœcium a suppression of one or more members of a whorl is most frequent in the andrœcium, while the perianth rarely consists of incomplete whorls (*Polygala*). Multiplication of the members of a whorl occurs most often in the andrœcium, less frequently in the gynœcium (*Malva*), still less frequently in the perianth (*Dryas octopetala*). Flowers with incomplete whorls, resulting unquestionably from suppression, are met with, for example, in the family *Scrophulariaceae*, in which the genus *Verbascum* possesses five fertile stamens, while in *Scrophularia* the posterior stamen is represented only by a staminodium, and in most of the other genera it is altogether absent. The origin of a pleiomerous whorl from one consisting of fewer members is equally well shown in the flowers of *Tilia*, where the numerous stamens are arranged in five groups, which occupy a corresponding position to the five simple stamens of allied forms.

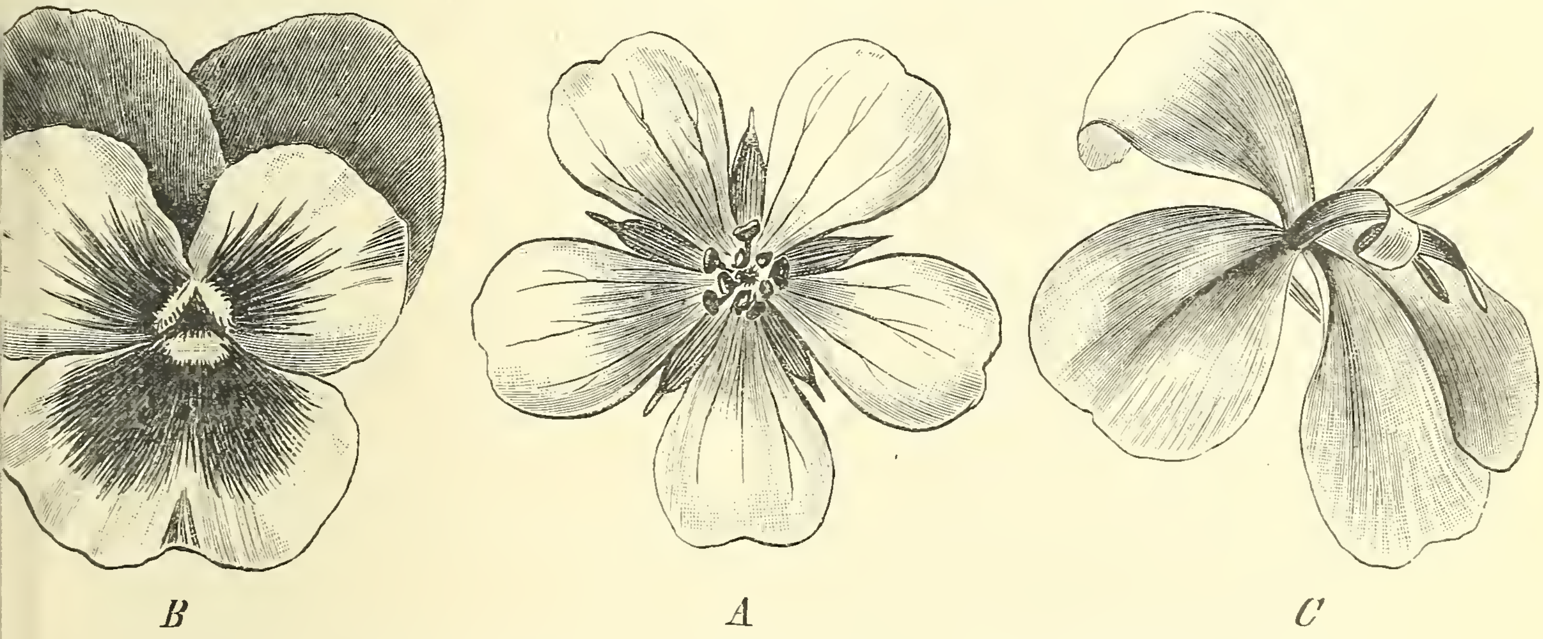


FIG. 378.—*A*, Actinomorphic flower of *Geranium sanguineum*. *B*, Zygomorphic flower of *Viola tricolor*. *C*, Asymmetrical flower of *Canna indica*.

The Symmetry of the Flower.—The flowers of Angiosperms are sometimes ACTINOMORPHIC (RADIAL) (Fig. 378, *A*), sometimes ZYGOMORPHIC (MONOSYMMETRICAL) (Fig. 378, *B*), or, more rarely, ASYMMETRICAL (Fig. 378, *C*).

Radial flowers exhibit probably the more primitive structure, since in them the arrangement of the members varies less from that of the vegetative region. The derivative origin of zygomorphic flowers is apparent in their more complicated structure, metamorphosis, and reduction. Zygomorphism is always indicative of a high degree of adaptation to insect-pollination.

A flower is LONGITUDINALLY ZYGOMORPHIC when the plane of symmetry coincides with the median plane of the flower, viz. the plane passing through its axis and the axis of the main stem (*e.g. Orchidaceae*, *Labiatae*, Fig. 379, *A*) ; OBLIQUELY ZYGOMORPHIC when it cuts the median plane at an acute angle (*Aesculus*, Fig. 379, *B*); TRANSVERSELY ZYGOMORPHIC when it cuts the median plane at right angles (*Fumariaceae*, Fig. 379, *C*). The first is by far the commonest. Occasionally a plant which otherwise possesses only zygomorphic flowers produces others of a radial structure. Such exceptional radial flowers are termed PELORIA, and are regarded as the result of reversion to the primitive type.

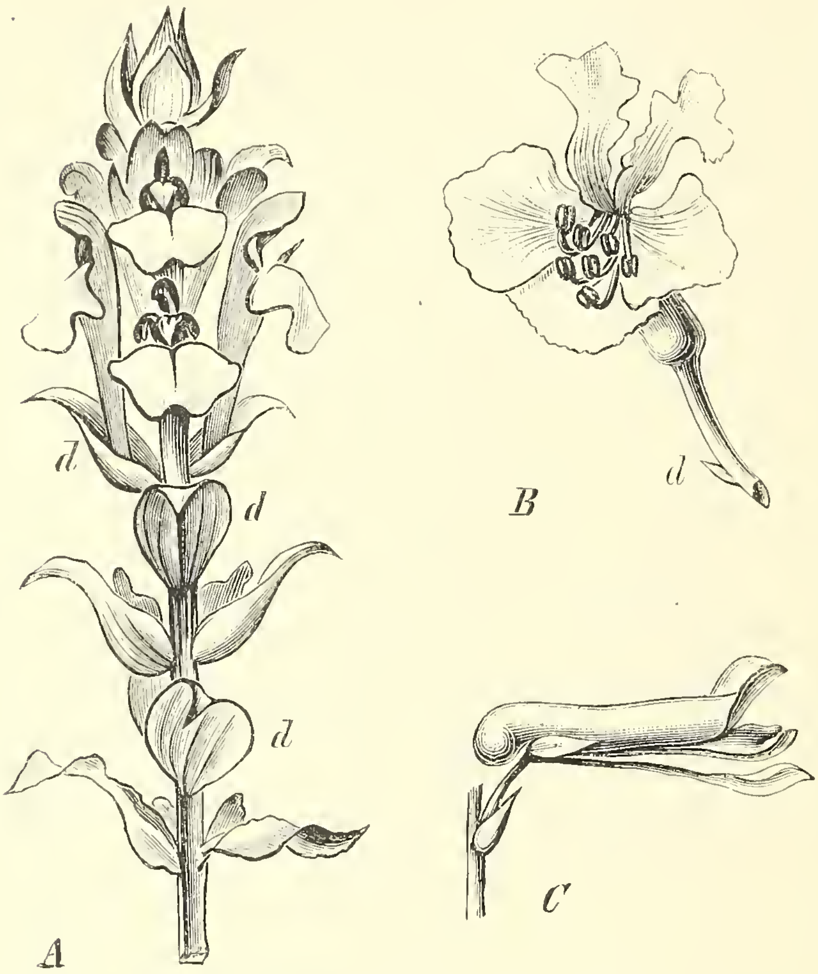


Fig. 379.—Flowers of, *A*, *Scutellaria alpina*, longitudinally zygomorphic; *B*, *Aesculus hippocastanum*, obliquely zygomorphic; *C*, *Corydalis lutea*, transversely zygomorphic; *d*, bracts.

Floral Diagrams and Formulæ (7).—The number and arrangement of the floral leaves are most clearly represented by means of diagrams or formulæ. The manner in which such diagrams may be constructed has previously been explained (p. 38). In a floral formula the single whorls are indicated by letters, the number of their members by corresponding figures, or, when their number is large or indefinite, by ∞. The union of parts is expressed by ( ), superior and inferior ovaries by a line above or below the corresponding figure, zygomorphism by ↑.

Of the letters employed in such formulæ, K = calyx, C = corolla, P = perigone, A = andrœcium, G = gynœcium. The following are examples of floral formulæ.

Lily	$P\ 3 + 3,\ A\ 3 + 3,\ G\ (\underline{3})$.
Buttercup . .	$K\ 5,\ C\ 5,\ A\ \infty,\ G\ \underline{\infty}$.
Apple Blossom .	$K\ 5,\ C\ 5,\ A\ \infty,\ G\ (\overline{5})$.
Digitalis . . .	$\uparrow K\ 5,\ C\ 5,\ A\ 4,\ G\ (\underline{2})$.

The Inflorescence (8)

The flowering shoot frequently bears only a single flower, which may then be either axillary or terminal. In many cases, however, the metamorphosis of the generative region, which results in the production of flowers, has led to the formation of a special system of fertile shoots termed an INFLORESCENCE or, after the fruit is formed, an INFRUCTESCENCE. Such inflorescences are wanting or ill developed among the Gymnosperms, while in the Angiosperms they are often well differentiated, constituting unities of a higher order.

The modifications exhibited by the fertile shoots of such an inflorescence are due, partly to a difference in their mode of branching, partly to the reduction or the metamorphosis of their leaves. These changes are the result of an adaptation to pollination, in the endeavour to aggregate the flowers and at the same time render them more conspicuous by the reduction of the foliage-leaves. Sometimes the whole system of fertile shoots is converted into an attractive apparatus, as in the *Araceae*, where the axis and the subtending leaf of the inflorescence have assumed the function, usually exercised by the perianth, of enticing insects.

Viewed from a purely morphological standpoint, two types of inflorescences may be distinguished, the BOTRYOSE (RACEMOSE, MONOPODIAL) and the CYMOSE (SYMPODIAL).

I. **Botryose Inflorescences.**—The main axis branches more vigorously than the lateral axis.

A. LATERAL AXES UNBRANCHED

(*a*) The RACEME.—The main axis is elongated and bears stalked flowers (Figs. 380 *B*, 381).

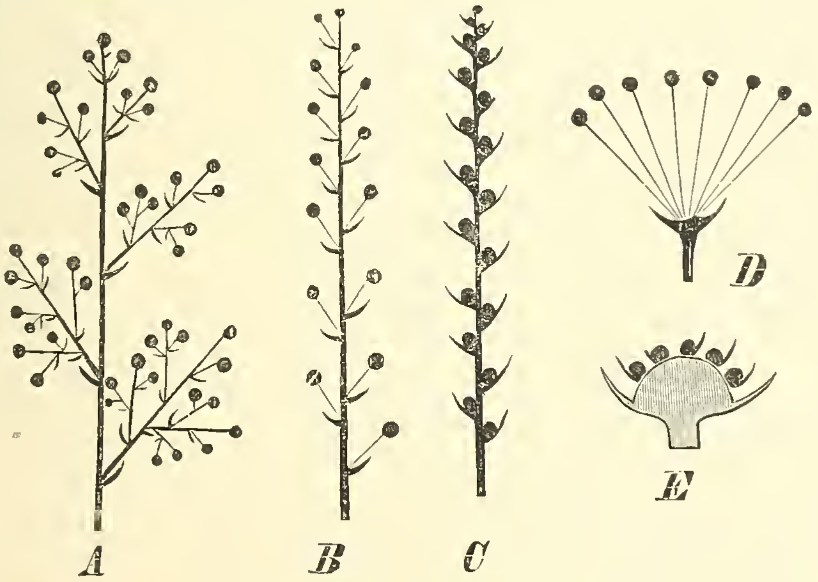


FIG. 380.—Diagrams of racemose inflorescences. *A*, Panicle; *B*, raceme; *C*, spike; *D*, umbel; *E*, capitulum.

(*b*) The SPIKE.—The main axis is elongated and bears sessile flowers (Figs. 380 *C*, 382).

A SPADIX is a spike with a fleshy axis; a CATKIN (Fig. 383), a spike which, after flowering or when the fruit is ripe, falls as a whole from the plant.

(*c*) The UMBEL.—The main axis is contracted and bears stalked flowers (Figs. 380 *D*, 384).

(*d*) The CAPITULUM.—The main axis is contracted and bears sessile flowers (Fig. 380 *E*).

B. LATERAL AXES BRANCHED

(*e*) The PANICLE.—In the panicle, as the term is generally used, the main axis is longer than the lateral axis, the whole inflorescence being correspondingly elongated (Figs. 380 *A*, 385).

A CORYMB is a flattened panicle; an ANTHELA a panicle in which the lateral axes overtop the central axis.

FIG. 381.
Raceme of *Linaria striata*.
d, bracts.

FIG. 382.
Spike of *Plantago lanceolata*.
(After DUCHARTRE.)

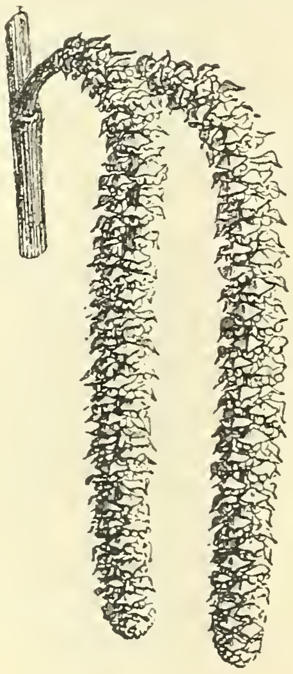


FIG. 383.
Catkin of *Corylus Americana*.
(After DUCHARTRE.)

II. Cymose Inflorescences.—The lateral axes grow more vigorously than the main axis for the time being, and form a pseudaxis.

(*a*) The MONOCHASIUM.—Each relative main axis produces only one branch.

A monochasium is termed a HELICOID CYME or BOSTRYX when the lateral branches always arise on the same side of the pseudaxis (Fig. 386 *C*), a SCORPIOID CYME or CINCINNUS when they occur alternately on opposite sides (Figs. 386 *B*, 388).

(*b*) The DICHASIUM.—Each relative main axis produces two branches (Figs. 386 *A*, 387).

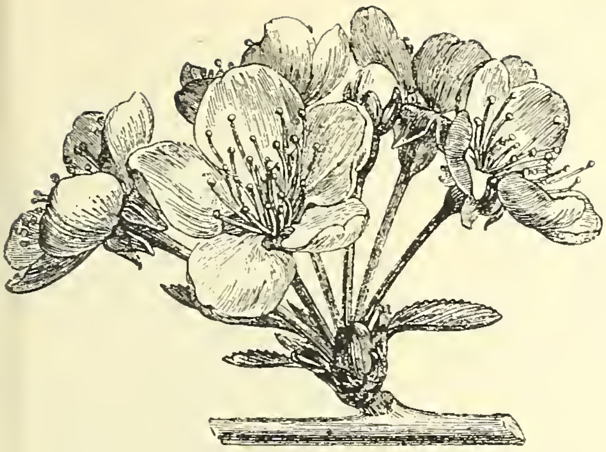


FIG. 384.—Umbel of the Cherry. (After DUCHARTRE.)

FIG. 387.—Cymose inflorescence (dichasium) of *Cerastium collinum ; t-t''''*, successive axes. (After DUCHARTRE.)

FIG. 385.—Panicle of *Yucca filamentosa*. (Reduced.)

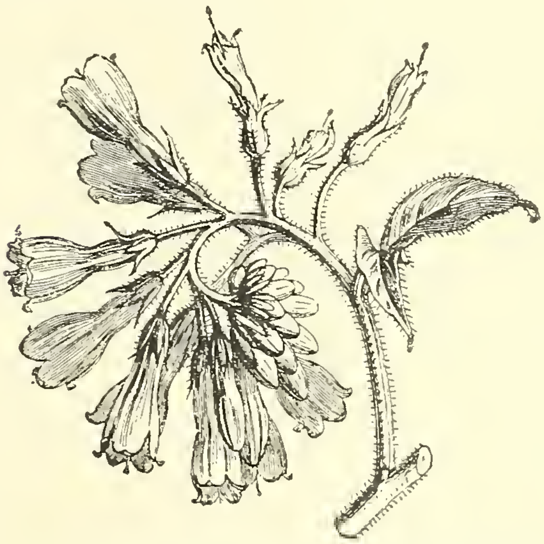


FIG. 388.—Scorpioid cyme of *Symphytum asperrimum*. (After DUCHARTRE.)

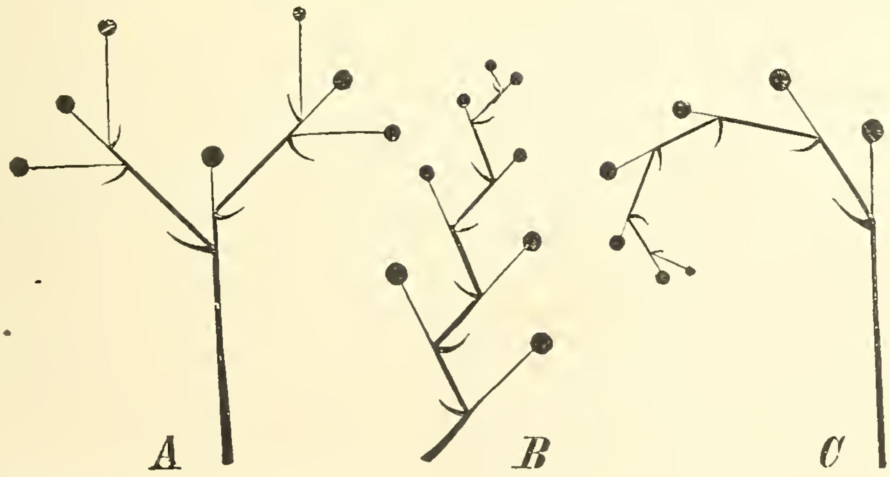


FIG. 386.—Diagrams of cymose inflorescences. *A*, Dichasium ; *B*, cincinnus, or scorpioid cyme ; *C*, bostryx, or helicoid cyme.

(*c*) The PLEIOCHASIUM.—Each relative main axis produces more than two branches.

Cymose frequently resemble racemose inflorescences, and are then termed CYMOSE PANICLES, CYMOSE SPIKES, CYMOSE RACEMES, etc.

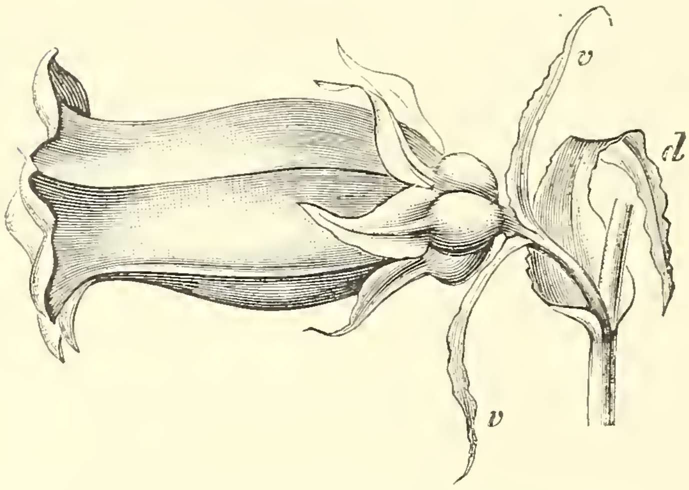


FIG. 389.—Flower of *Campanula medium* with bract (*d*) and bracteoles (*v*).

The fleshy portion of the Fig corresponds to a highly ramified, cymose branch-system, and must therefore be classified here.

By the further branching of an inflorescence, compound inflorescences may occur which are constructed after the same type (*e.g.* the compound umbel of the *Umbelliferae*), or consist of a union of several types (*e.g.* the corymbs of *Achillaea* formed by an aggregation of capitula).

An inflorescence is also usually provided with more or less reduced bracteal leaves or hypsophylls; those from the axil of which a flower or flowering shoot springs are called SUBTENDING LEAVES or BRACTS, while the leaves borne on the stalks of the flowers are designated BRACTEOLES or PROPHYLLA (Fig. 389).

Some examples may be added to the preceding general account of the phylogeny of the flower. Taking the most primitive of living Gymnosperms first, we find that *Cycas*, the habit of which recalls a tree fern, is diœcious. The male tree produces in the axils of the large pinnate leaves several male flowers, each of which is a short lateral shoot, the basal portion forming the stalk of attachment to the stem. The stamens are large scales bearing a considerable number of pollen-sacs on the lower surface.

The female flower of *Cycas* is not a lateral branch; the main axis of the female tree flowers periodically. In place of vegetative leaves, carpels arise at the growing point, and these, arranged in close spirals over a definite region of the stem, form the female flower. The carpels are not green, much smaller than the foliage leaves, and thickly covered with brown hairs. They resemble the foliage leaves more than the stamens in form, being of large size, pinnate above, and bearing the ovules, which attain the size of a cherry, laterally towards the base.

The male flowers are nearly as simply constructed in the *Coniferae*, to which higher group of Gymnosperms most of the existing forms belong. Their stamens are scale-like and usually bear a definite number of pollen-sacs. The construction of the female flowers and inflorescences is less simple, so that difficulties have arisen in the interpretation of their morphology. In them also, however, scale-like structures bear the ovules, which are usually definite in number.

In the *Gnetaceae*, to which the highest position in the system of classification of the Gymnosperms is accorded, an approximation to the Angiospermic flower is to be seen (*e.g.* in *Ephedra*). The floral axis is short, a perianth is developed, and both sexes are united in the same flower.

It is a doubtful question which Angiosperms are to be regarded as the most primitive, since palæontology affords no clear evidence on the point. The *Polycarpieae* are often taken as the original type of the Dicotyledons and the *Liliaceae* of the Monocotyledons. On the other hand, this place is often given to those forms with small unisexual flowers, a sepaloid perianth, and an indefinite number of stamens and carpels in the flower, *e.g.* the simplest *Helobieae* and *Amentaceae.*

Great complications enter into the phylogenetic development of the Angiosperms owing to the increase in number, suppression, and union of the members of the flower; the occurrence of zygomorphy and the aggregation of flowers into unities of a higher order are further causes of difficulty. The most highly organised zygomorphic flowers are found in the *Orchidaceae* and *Zingiberaceae* and are described in the special part. In this place the relatively simple flowers of the *Scrophulariaceae* and *Labiatae* may be mentioned; *Salvia* is a striking example of the latter. The perianth is clearly divided into calyx and corolla, the component members of both whorls being coherent. The simply constructed calyx serves to protect the bud; the corolla is two-lipped by the unequal union of the petals. Of the five stamens, which the ancestral form, in common with the less highly differentiated relatives of these orders, possessed, one is completely suppressed, two are represented by staminodes, and two are present but developed in a peculiar manner. The two halves of the anther are separated by a great development of the connective; one of them is fertile, while the other theca forms a sterile lobe. The two carpels are divided into four chambers by deep constrictions. How wonderfully this structure stands in relation to the mode of pollination is evident from p. 286.

The *Compositae*, which are usually regarded as standing highest in the phylogenetic series of the Angiosperms, or at least of the larger sub-division, the Dicotyledons, afford the best example of the aggregation of the single flowers into unities of a higher order which are popularly called flowers. In *Chrysanthemum leucanthemum* the capitulum is surrounded by an involucre of bracts resembling a calyx; these bracts are quite different from the foliage leaves and, like a calyx, perform the function of protecting the young flower-buds. In other *Compositae* the involucre serves other purposes in addition, and has a more peculiar construction. The peripheral flowers of the head are zygomorphic, white in colour, and female, the central florets are yellow, actinomorphic, and hermaphrodite.

The Sexual Generation (9).—The sexual generation of the Phanerogams is closely comparable to that of the heterosporous Pteridophyta. As compared with the homosporous Pteridophyta it is very poorly developed; this is especially the case with the male prothallus.

Numerous mother cells of the pollen are formed in the pollen-sac, while only a single mother cell of the embryo-sac is developed in the nucellus. The pollen-grains are formed by the tetrad division of their mother cells. In many cases the mother cell of the embryo-sac also divides into four young embryo-sacs; in other cases three, or two young embryo-sacs arise, or the mother cell may be directly transformed into the embryo-sac. Even where several young embryo-sacs arise from the mother cell, only one continues its development.

The **Male Prothallium** (9) of the Gymnosperms resembles that of the heterosporous Pteridophyta in that a small cell is cut off laterally by a curved wall from the large pollen-cell; the latter is to be regarded as the vegetative cell of the prothallium, while the small cell corresponds to the rudiment of the antheridium. By one or two cell divisions parallel to the first, a chain of two or three cells may be formed. the innermost of which is the antheridial cell. This gives rise to two generative cells, which in the most primitive Gymnosperms (*Cycadaceae* Fig. 390, *Ginkgoaceae*) develop as spermatozoids (10), in the higher Gymnosperms as naked cells without cilia.

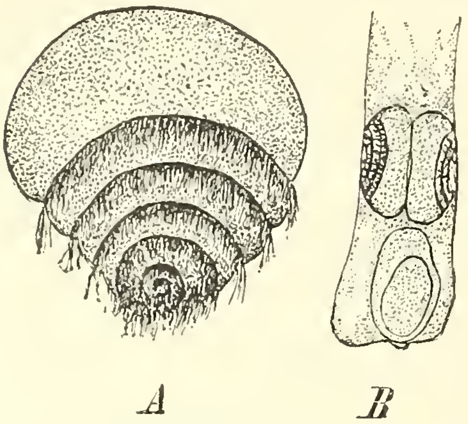


FIG. 390.—*A*, Spermatozoid of *Zamia integrifolia*. (× 90.) *B*, End of a pollen-tube just before fertilisation, showing the two spermatozoids and the stalk-cell. (× 50.) (After WEBBER.)

The **Male Sexual Generation** of the Angiosperms (9) shows a further reduction as compared with the Gymnosperms. A small antheridial cell is separated from the pollen-cell (Fig. 391), but no cell wall forms between the two, and a row of cells is never developed. The antheridial cell divides into two male sexual cells; spermatozoids are not formed.

The **Female Sexual Generation** (9) of the **Gymnosperms** is closely connected with that of the heterosporous Pteridophytes, especially with *Selaginella*. As in the latter genus, numerous nuclei are first formed by free nuclear division, which arrange themselves around the wall of the embryo-sac; by the later formation of partition walls a parenchymatous tissue is formed which gradually fills the embryo-sac. Archegonia arise from some of the superficial cells of the upper end of the prothallus. The archegonia while constructed on the same plan are more simple than in the Pteridophyta; they consist of a ventral portion enclosing the ovum, the neck consisting of a few cells, and the ventral canal cell, which lies just below the neck. Only the neck canal cells are wanting (Fig. 392).

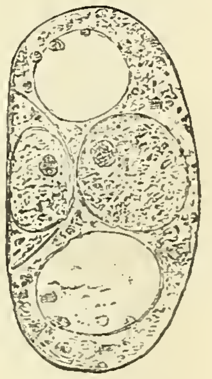


FIG. 391.—*Tradescantia virginica*. Pollen-grain after division into an antheridial and vegetative cell. (× 540.)

In the **Fertilisation** of the **Gymnosperms** (9) the pollen-grain, which has been carried by the wind to the micropyle of the ovule and has thence passed into a depression of the summit of the nucellus (the pollen-chamber), puts out a pollen-tube. In the formation of this the intine alone takes part, the exine being simply broken through. A pollen-tube of this kind is characteristic of all Phanerogams which ENGLER has therefore termed Siphonogams (*Embryophyta Siphonogama*).

The male sexual cells pass into the growing pollen-tube. The latter, influenced by chemotactic stimuli, grows down into the tissue of the nucellus until it reaches an archegonium. It bores through the short neck of the archegonium, and its tip penetrates to the ovum.

On one of the sexual cells fusing with the ovum, fertilisation is effected; the most obvious feature of this is the union of the male nucleus with the nucleus of the ovum.

The *Gnetaceae*, which we have already seen to be the most highly developed and the most recent Gymnosperms, show important and interesting peculiarities in the development and structure of their female prothallium. Of the three genera forming the order, *Ephedra* agrees entirely with the coniferous type, in *Welwitschia* the archegonium is reduced to a single cell, while in *Gnetum* (11), which produces a number of macrospores, the archegonia are entirely wanting. A prothallium may be formed in the basal portion of the embryo-sac (*Gn. Gnemon*) or may be entirely wanting. The layer of protoplasm lining the embryo-sac contains numerous free nuclei which are capable of fertilisation; several are fertilised, since more than one pollen-tube reaches the embryo-sac, and each of the two generative nuclei conjugates with one of the egg-nuclei. After fertilisation a more or less abundant formation of endosperm takes place round the growing zygotes. Only one of the embryos reaches full development in each ovule.

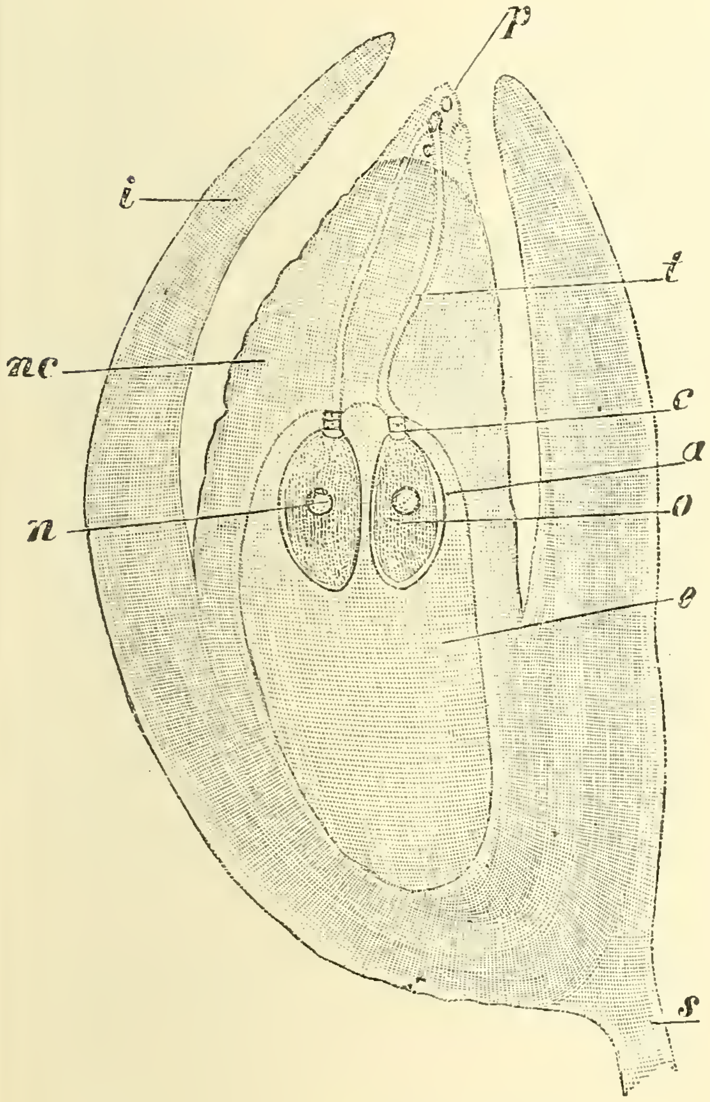


FIG. 392.—Median longitudinal section of an ovule of *Picea vulgaris*. *e*, Embryo-sac filled with endosperm; *a*, archegonium showing ventral (*o*) and neck portion (*c*); *n*, nucleus of egg-cell; *nc*, nucellus; *p*, pollen-grains; *t*, pollen-tube; *i*, integument; *s*, seed-wing.

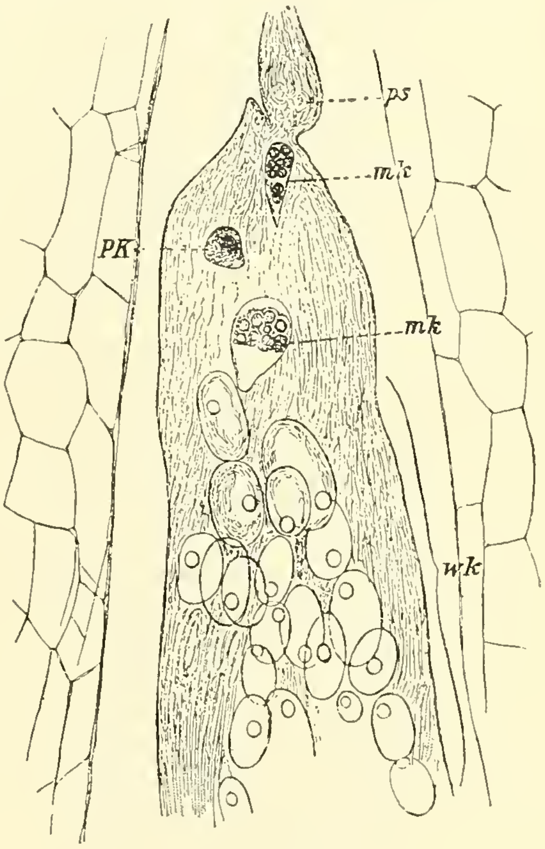


FIG. 393.—Embryo-sac of *Gnetum* shortly before the conjugation of nuclei takes place. *ps*, apex of a pollen-tube; *mk*, male nuclei; *wk*, female nuclei; *pk*, disorganised nucleus of the pollen-tube. (After G. KARSTEN. × 325.)

The **Female Sexual Generation of the Angiosperms** (9) is much further reduced than that of the Gymnosperms, and differs both in its mode of origin and in its mature state more from the latter than does the female prothallus of the Gymnosperms from that of *Selaginella.*

The ovule usually contains only a single embryo-sac. Within the latter there are not, as in the Gymnosperms, numerous cells forming a continuous tissue, but only six cells, which are found in groups of three at either pole of the embryo-sac, and remain naked until fertilisation.

The group at the micropylar end of the embryo-sac is termed the egg-apparatus. It consists of the OVUM and of two cells, which remain sterile, and on account of the part they play in the process of fertilisation are called SYNERGIDÆ. The cells at the opposite pole of the embryo-sac are called ANTIPODAL CELLS.

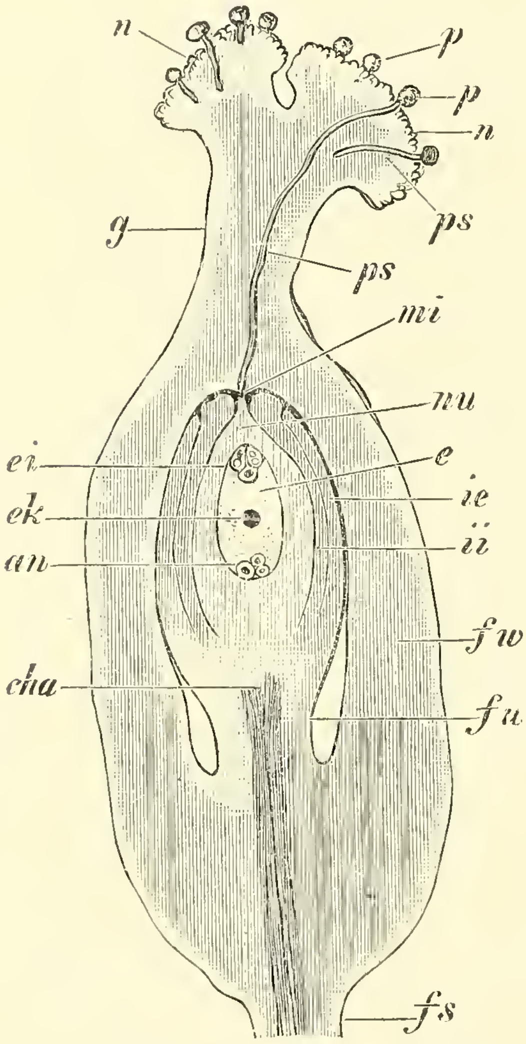


FIG. 394.—Ovary of *Polygonum Convolvulus* during fertilisation. *fs*, Stalk-like base of ovary; *fu*, funiculus; *cha*, chalaza; *nu*, nucellus; *mi*, micropyle; *ii*, inner, *ie*, outer integument; *e*, embryo-sac; *ek*, nucleus of embryo-sac; *ei*, egg-apparatus; *an*, antipodal cells; *g*, style; *n*, stigma; *p*, pollen-grains; *ps*, pollen-tubes. (×48.)

The egg-apparatus and antipodal cells originate in this way. The nucleus of the embryo-sac divides into two. Of these, one moves towards the upper micropylar pole, the other towards the lower or chalazal pole. Each nucleus then gives rise by repeated division to four nuclei, around three of which protoplasm becomes aggregated, while the remaining two nuclei, withdrawing towards the centre of the embryo-sac, meet and fuse into the definitive or secondary nucleus of the embryo-sac. The three naked cells at the micropylar end develop into the egg-apparatus, the three at the chalazal end into the antipodal cells.

Fertilisation in the Angiosperms (9).—While in the Gymnosperms the pollen-grains germinate on the summit of the nucellus, this takes place in Angiosperms on the stigma; the pollen-tube has thus to traverse a considerable distance through the stigma, the style, and the cavity of the ovary before the ovum is reached. Usually the pollen-tube gains entrance to the ovule by the micropyle (Fig. 394); in several groups of Angiosperms, however (*Choripetalae*, *Compositae*), cases are known in which the pollen-tube makes its way through the funiculus or the integuments (Fig. 395) and reaches the embryo-sac by the chalazal end (12). As a rule special conducting tracts (13) are present on the wall of the ovary and at the funiculus which bring the apex of the pollen-tube to the vicinity of the micropyle, where chemotropic influences determine its entrance. The apex of the tube thus reaches the synergidæ (Fig. 396). One of the two generative cells penetrates into the ovum, and fertilisation is effected by the fusion of the two nuclei. The synergidæ disintegrate,

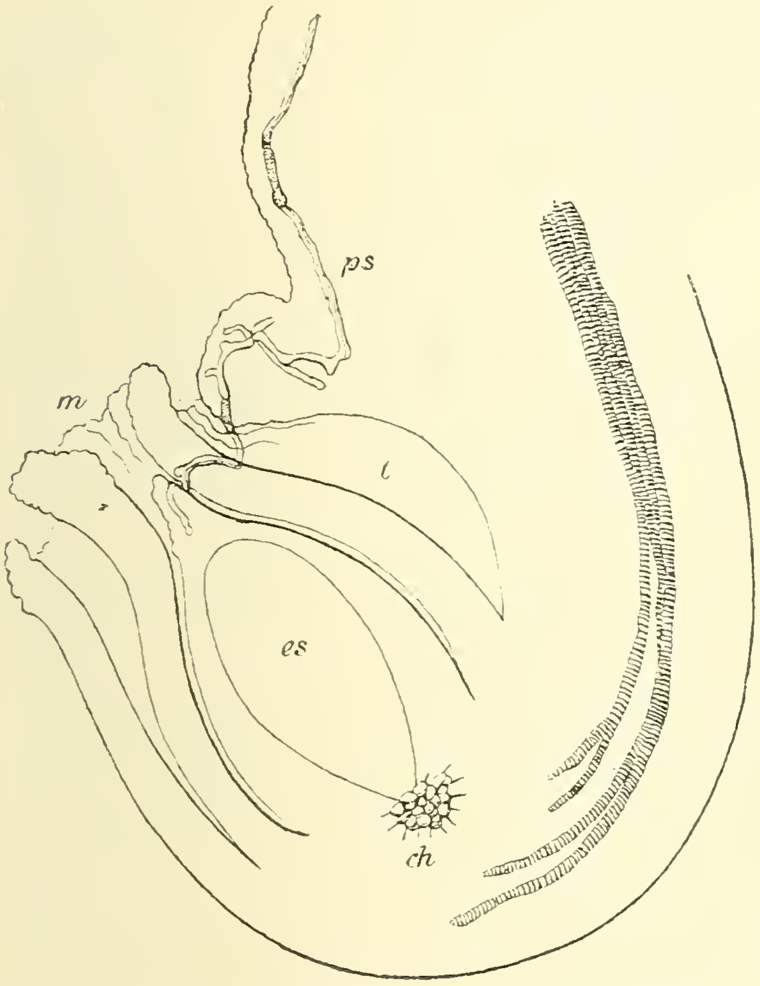


Fig. 395.—Ovule of *Ulmus pedunculata*. *es*, Embryo-sac ; *m*, micropyle ; *ch*, chalaza ; *t*, pocket-like space between the integuments. The pollen-tube, *ps*, penetrates directly through the two integuments and reaches the apex of the nucellus. (After Nawaschin.)

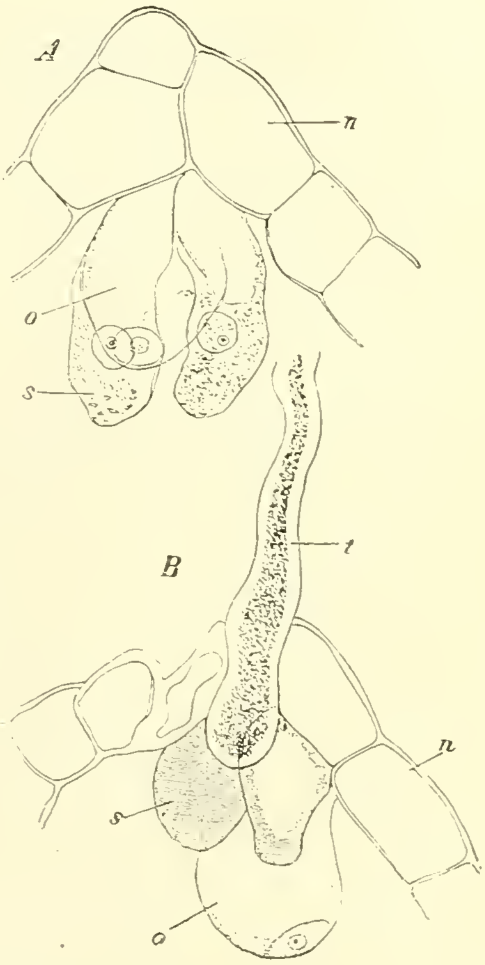


Fig. 396.—*Funkia ovata.* Apex of nucellus, showing part of embryo-sac and egg-apparatus. *A*, Before, *B*, during fertilisation ; *o*, egg-cell ; *s*, synergidæ ; *t*, pollen-tube ; *n*, nucellus. (× 390.)

while the fertilised ovum surrounds itself with a cell wall, and as a rule forms a row of cells separated by transverse walls, the proembryo. The terminal cell of the proembryo gives rise to nearly the whole of the young plant.

According to the investigations of Nawaschin, Guignard (14), and others, one of the two elongated, spirally-wound, vermiform male nuclei fuses in the Angiosperms with the nucleus of the ovum ; the other fuses with the two polar nuclei of the embryo-sac or with the definitive nucleus resulting from the previous fusion of these (Fig. 397). After this fusion the formation of the endosperm commences.

During the development of the embryo a parenchymatous tissue, termed the ENDOSPERM, is formed within the embryo-sac, usually completely filling its remaining free space ; this arises by a process of multicellular formation preceded by free nuclear division or by repeated cell-division. In some species of plants the endosperm is completely disorganised and supplanted by the growing embryo; in other cases it occupies a larger or smaller part of the ripe seed.

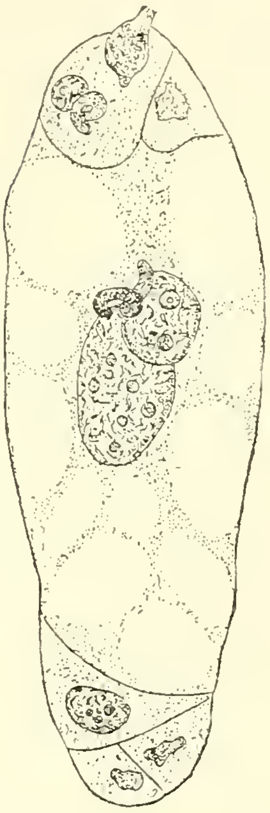


FIG. 397.—Fertilisation of *Lilium Martagon*. One of the male nuclei is close to the nucleus of the ovum, the other is in contact with the nuclei of the embryo-sac.

Important differences from the usual state of things are found, according to TREUB (15), in *Casuarina*, a genus which is the representative of a very peculiar type. This plant possesses, in contrast to the other Angiosperms, a bulky sporogenous tissue from which a large number of embryo-sacs arise. Each of the latter contains an egg-apparatus, consisting of 1-3 cells, which are derived from a single mother cell. The "neighbouring cells" when present have more in common with canal-cells than with synergidæ. There are no antipodal cells. The formation of the endosperm has already started by the free formation of nuclei in the lining layer of cytoplasm before fertilisation has taken place.

Further Development of the Fertilised Ovum. The Embryo (9, 16).—The fertilised ovum soon undergoes divisions and develops into the embryo. In the GYMNOSPERMS the nucleus of the embryo resulting from the fusion of the male and female nuclei undergoes repeated divisions in the end of the egg-cell opposite the neck of the archegonium. Four cells are thus produced lying in the same plane, which by transverse divisions give rise to several tiers of cells (Fig. 398, *D-F*). The four cells of one of the upper tiers elongate into four long tubes, and push the cells destined to become the rudiments of an embryo deep into the tissue of the prothallium. From these, by further division, either a single embryo arises or, by the longitudinal division of the embryonic rudiment, four embryos are formed, only one of which, however, attains its full development.

At first the embryo is a mass of cells showing neither external nor internal differentiation. As it develops it exhibits, owing to the unequal growth of its parts, an external segmentation, which corresponds to an internal differentiation of its tissues. In an old embryo it is possible to distinguish the unbranched radicle, the tip of which is directed upwards, the hypocotyledonary stem, and the cotyledons, which differ in form from the later leaves. The number of cotyledons is not constant in the Gymnosperms; it may be two or several. The minute bud, which occupies the apex of the embryo and is surrounded by the cotyledons, is the plumule from which the further development of the shoot proceeds. This embryo is very similar in its differentiation into members to that of *Selaginella*.

In the ANGIOSPERMS the fertilised ovum surrounds itself with a cell wall and becomes converted into the proembryo by successive transverse divisions. The terminal cell of the proembryo forms the main part of the embryo, the adjoining cell contributing also, while the other cells form the suspensor. As in the Gymnosperms, the suspensor elongates and often shows special adaptations for the nutrition of the embryo. The latter is represented at first by a multicellular sphere terminating the filiform SUSPENSOR, and becomes differentiated, generally before the seed is ripe, into a radicle, hypocotyl, and one or two cotyledons. The number of cotyledons developed is, as a rule, constant and furnishes the most characteristic, although by no means the only method of distinguishing the two divisions of the Angiosperms, which are accordingly termed Monocotyledons and Dicotyledons.

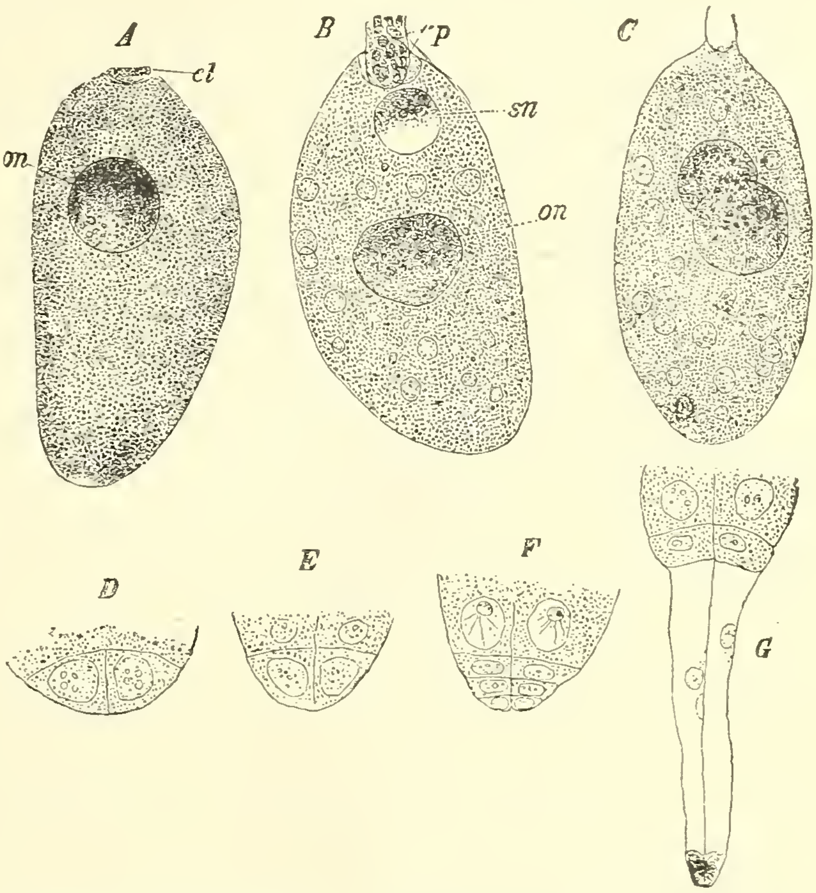


FIG. 398.—*Picea vulgaris*. *A*, Egg-cell with nucleus (*on*) and ventral canal-cell (*cl*); *B*, egg-cell in process of fertilisation; *on*, nucleus of egg; *sn*, the male nucleus which has passed from the pollen-tube (*p*) into the egg-cell; *C*, later stage, showing the two nuclei in process of fusion; *D*, lower part of egg, showing two of the four nuclei; *E*, *F*, successive stages, resulting in the formation of four rows of cells (two only visible) arranged in tiers; *G*, the cells of the middle tier have elongated and pushed the lower tier of cells, which have undergone division, into the endosperm. (×90.)

The embryo shows so much variation, not only in both divisions of the Angiosperms, but within the different families, that no general scheme of embryonic development can be given. In many Dicotyledons, for example in *Capsella bursa pastoris* (Fig. 399), where the development of the embryo is particularly easy to follow, the end of the proembryo farthest removed from the micropyle is converted into a row of cells by the formation of transverse walls. The terminal cell expands into a sphere, and, undergoing division, becomes divided into octants. Each octant cell is further divided by periclinal walls into an outer and an inner cell. The outer cells form the epidermis; the inner, by continued division, give rise to the fundamental tissue and the vascular bundles. The upper half of the sphere develops into the cotyledons and plumule, the lower half into the hypocotyl and root. The root is derived in part also from the HYPOPHYSIS, a cell resulting from the transverse division of the next adjoining cell of the suspensor.

The cotyledons first appear as protuberances from the upper half of the sphere. The plumule does not become differentiated until later.

In Monocotyledons the single cotyledon is usually developed at the apex of the embryo (Fig. 400); but in some cases (*Dioscoreaceae*) it arises laterally, as in the Dicotyledons.

ADVENTITIOUS EMBRYOS are sometimes produced by both Dicotyledons and Monocotyledons (*e.g. Funkia ovata*) by the budding of cells of the nucellus in the neighbourhood of the egg-apparatus. The fertilised egg, as a rule, does not then continue its development. In the case of *Coelebogyne*, adventitious embryos are formed even when no fertilisation of the egg has taken place. Seeds in a ripe condition, which contain several such adventitious embryos, afford examples of POLYEMBRYONY (17). Ovules provided with several embryo-sacs do not exhibit polyembryony, as in that case only one embryo attains full development.

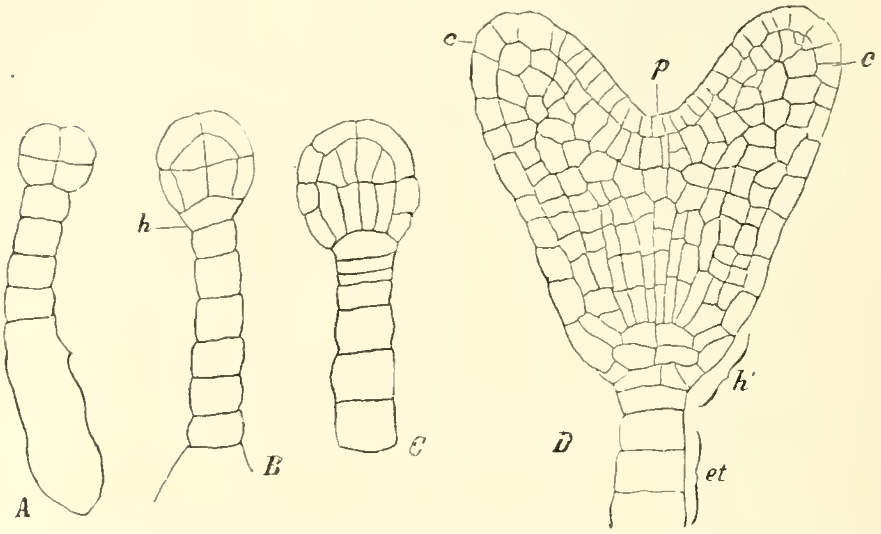


FIG. 399.—Stages in the development of the embryo of *Capsella bursa pastoris* (*A-D*). *h*, Hypophysis; *et*, suspensor; *c*, cotyledons; *p*, plumule. (After HANSTEIN, magnified.)

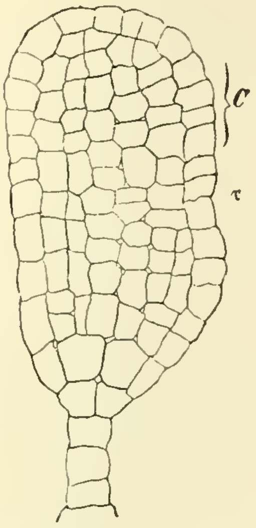


FIG. 400.—Young embryo of *Alisma Plantago*. *C*, Cotyledon; *v*, growing point. (After HANSTEIN, magnified.)

The formation of the embryo is not, as in the Gymnosperms, the only result of fertilisation. In the Gymnosperms those male nuclei which do not fuse with the ovum simply disintegrate. In Angiosperms, however, as NAWASCHIN and GUIGNARD first showed, THE SECOND OF THE TWO SPERM-NUCLEI DERIVED FROM THE POLLEN-GRAIN FUSES WITH THE NUCLEUS OF THE EMBRYO-SAC. After this fusion the nucleus of the embryo-sac divides into two. Repeated cell division or free nuclear division follows, and leads to the formation of a parenchymatous tissue, the ENDOSPERM, filling the embryo-sac. The formation of this tissue may be regarded as a continuation of the interrupted development of the prothallium, which in Gymnosperms is completely formed before fertilisation. The result in both cases is the filling of the embryo-sac with a nutritive tissue.

The Seed (18).—After the embryo has attained a definite stage of development, varying in different species, its further growth ceases, and parting with its constituent water, it passes into a dormant condition, from which, after the lapse of a longer or shorter period, it emerges only when abundantly supplied with water. The other parts of the ovule also increase in size, after fertilisation has been effected, and undergo extensive internal modification. As a result of the changes incident upon fertilisation, the ovule becomes converted into a SEED.

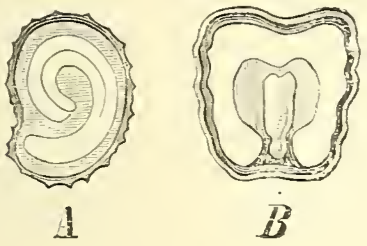


FIG. 401.—*A*, Seed of *Hyoscyamus niger*, showing the Dicotyledonous embryo embedded in the endosperm ; *B*, seed of *Elettaria Cardamomum*, enveloped by a thin aril ; the white, mealy perisperm next to the seed-coat encloses an oleaginous endosperm (shaded), in which the Monocotyledonous embryo lies embedded. (After BERG and SCHMIDT, magnified.)

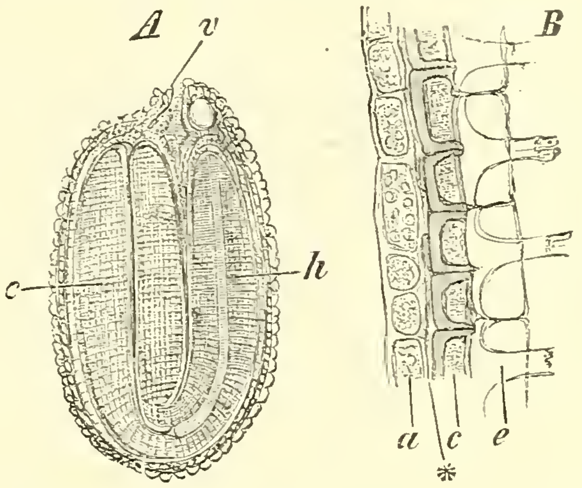


FIG. 402.—*Capsella bursa pastoris*. *A*, Longitudinal section of a ripe seed ; *h*, hypocotyl; *c*, cotyledons ; *v*, vascular bundle of the funicle (× 26) ; *B*, longitudinal section of the seed-coat after treatment with water ; *e*, the swollen epidermis; *c*, brown, strongly thickened layer ; *, compressed layer of cells ; *a*, aleurone grains (× 240.)

THE DEVELOPMENT OF SEEDS, OR ENCLOSED MACROSPORANGIA CONTAINING EMBRYOS, IS A DISTINCTIVE CHARACTERISTIC OF THE PHANEROGAMS. In conformity with this distinction, they are also termed SEED-PLANTS or SPERMAPHYTES.

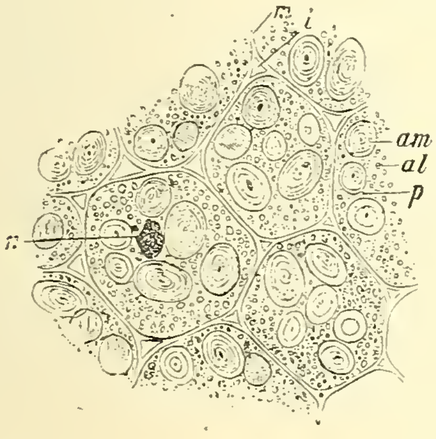


FIG. 403.—Part of section through one of the cotyledons of the Pea, showing cells with reserve material. *am*, Starch grains ; *al*, aleurone grains ; *p*, protoplasm ; *n*, nucleus.

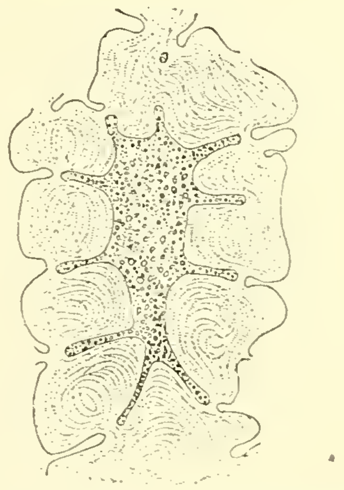


FIG. 404.—Cell from the endosperm of *Phytelephas macrocarpa*, with reserve cellulose. (× 225).

The essential parts of the seed, which are always present, are the seed-coats developed from the integuments of the ovule and the embryo (Fig. 402). Frequently a parenchyma rich in nutritive material is formed between the embryo and the seed-coats. When this nutritive tissue, or so-called ALBUMEN, is derived from the nucellus, it is termed the PERISPERM (Fig. 401, *B*); when developed within the embryo-sac, the ENDOSPERM (*A*). If the seed is provided with neither endosperm nor perisperm (Fig. 402, *A*), the cells of the embryo itself are filled with accumulated reserve material. The endosperm, or, in its absence, the tissue of the cotyledons, is usually thin-walled (Fig. 403); the cells are filled with aleurone grains, starch, and oil. Sometimes, as in the endosperm of *Phytelephas macrocarpa*, which is called vegetable ivory from its extreme hardness, the cell walls are greatly thickened and consist of nearly pure cellulose (Fig. 404). On germination these various reserve materials are converted by the action of ferments into diffusible substances (*e.g.* sugars, amides, etc.) for the nourishment of the young plant.

The seed-coat is variously constructed, usually hard and dry; on its smooth or variously sculptured surface the mark of attachment of the funiculus, the hilum (Fig. 406, *A*, *h*) is often visible. The micropyle also is often recognisable as a minute depression of the surface (Fig. 406, *B*, *m*). In certain cases an outer succulent covering, the ARILLUS (Figs. 405, 406, *D*), arises from the chalaza, or a smaller outgrowth morphologically equivalent to the arillus is present (CARUNCULA, Fig. 406, *B*, *C*).

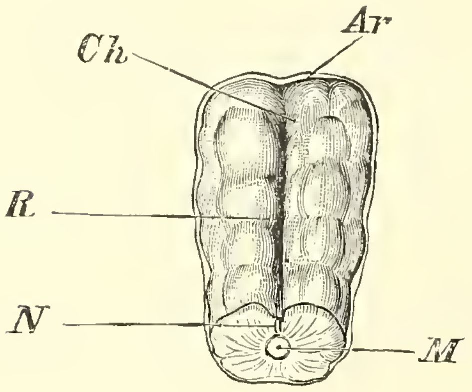


FIG. 405.—Seed of *Elettaria cardamomum*. *M*, Micropyle; *N*, hilum; *R*, raphe; *ch*, chalaza; *Ar*, arillus. (After A. MEYER, magnified.)

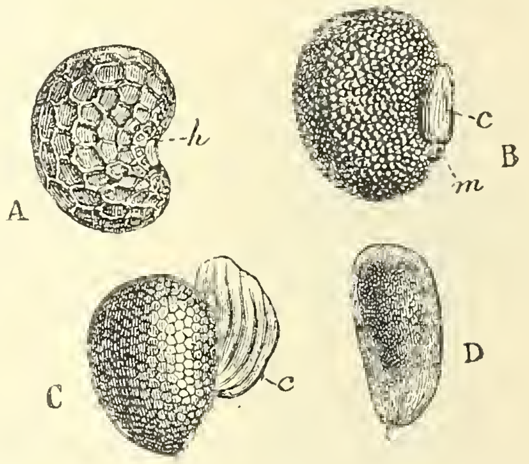


FIG. 406.—*A*, Seed of *Papaver Rhoeas*; *h*, the hilum: *B*, seed of *Corydalis ochroleuca*; *m*, micropyle; *c*, caruncula: *C*, seed of *Chelidonium majus*: *D*, seed of *Nymphaea alba* with its arillus. (After DUCHARTRE.)

The Fruit (^{18}).—The influence exerted by fertilisation is not restricted solely to the formation of the seed. Other parts of the flower also undergo modification and are adapted to new functions, such as the protection and dissemination of the seeds; while those parts which, after pollination, are no longer of service, ultimately wither.

THE PRODUCT OF THE CHANGES INDUCED BY FERTILISATION IN THE PERSISTENT PARTS OF THE FLOWER IS TERMED A *FRUIT*. The formation of fruit, as well as the development of seeds, is an essential characteristic of phanerogamic plants. Like the flower from which it is produced, the fruit may also have a more or less complicated structure. In the simplest cases it consists solely of the carpels (*e.g. Cruciferae*), which, with the seeds, always constitute the essential part of the fruit. Sometimes the flower-axis performs an important part in the formation of the flower, particularly in perigynous and epigynous flowers (*e.g.* Rose, Apple). Less frequently, the leaves of the perianth are transformed into part of the fruit, as in Spinach, when they form a hard, spinous envelope about the gynœcium. The androecium, on the other hand, always disappears after pollination has been accomplished.

The once prevalent custom of considering the fertilised gynœcium alone as the fruit is productive of great confusion. According to this view, only the central portion of an Apple, for example, constitutes the fruit; while the larger, peripheral portion, derived from the modified axis, would not be regarded as belonging to it. The definition of a fruit given above is that adopted by EICHLER.

The fruits of Gymnosperms are very simply constructed. The flower undergoes only a few changes in becoming a fruit; it increases in size, its carpels become harder and more strongly lignified, or, as in Juniper, they may become succulent.

The fruit of Angiosperms has a more varied and complicated structure. The fruit possesses a different structure according as it is derived from an apocarpous or a syncarpous gynœcium. In the first case the ripe carpels are separate and are termed FRUITS; in the second the carpels continue united, at least until the maturity of the fruit. A fruit of a more complicated structure occurs when other members of the flower than the gynœcium take part in its formation.

That part of the fruit enveloping the seeds, consisting sometimes of the carpels alone, sometimes of the carpels and the adherent receptacle, is termed the PERICARP or FRUIT-WALL. The pericarp frequently appears to be differentiated into zone-like layers of tissue. The outer layer is then termed the EXOCARP, the innermost the ENDOCARP, and the layer sometimes lying between them the MESOCARP.

According to the character of the pericarp and its condition at maturity, several varieties of fruit have been distinguished, of which the following are the most important.

I. **The Capsule.**—Fruit with a dry pericarp, dehiscing at maturity. Most frequently the carpels separate from one another by longitudinal slits (SEPTICIDAL DEHISCENCE), or each carpel is split in half longitudinally (LOCULICIDAL DEHISCENCE, Fig. 407, *B*). In more rare cases the seeds escape through pores (PORICIDAL DEHISCENCE, *e.g. Antirrhinum*, (Fig. 407, *C*).

The following distinctive forms of capsules have been recognised.

(*a*) THE FOLLICLE, consisting of a single carpel, which dehisces along the ventral suture (*Paeonia*, *Aconitum*).

(*b*) The LEGUME or POD, consisting of a single carpel, which, however, dehisces along both the ventral and dorsal suture (Pea, Bean, and many other *Leguminosae*).

(*c*) The SILIQUA, consisting of two carpels, which separate at maturity, leaving a persistent partition wall (the majority of the *Cruciferae*, *e.g. Capsella bursa pastoris*).

(*d*) The PYXIDIUM, opening at maturity with a lid-like valve (*Anagallis* (Fig. 407, *D*, *E*) *Hyoscyamus*).

II. Dry Indehiscent Fruit.—This type comprises fruits with a dry pericarp, which neither dehisce at maturity nor break up into separate carpels. Indehiscent fruits with a hard dry pericarp are termed NUTS (Fig. 408, *A*). An indehiscent fruit containing one seed and having a leathery pericarp is distinguished as a CARYOPSIS (Grasses) if the pericarp is adherent to the seed, if not it is termed an ACHENE (*Compositae*, *Fagopyrum*, Fig. 408).

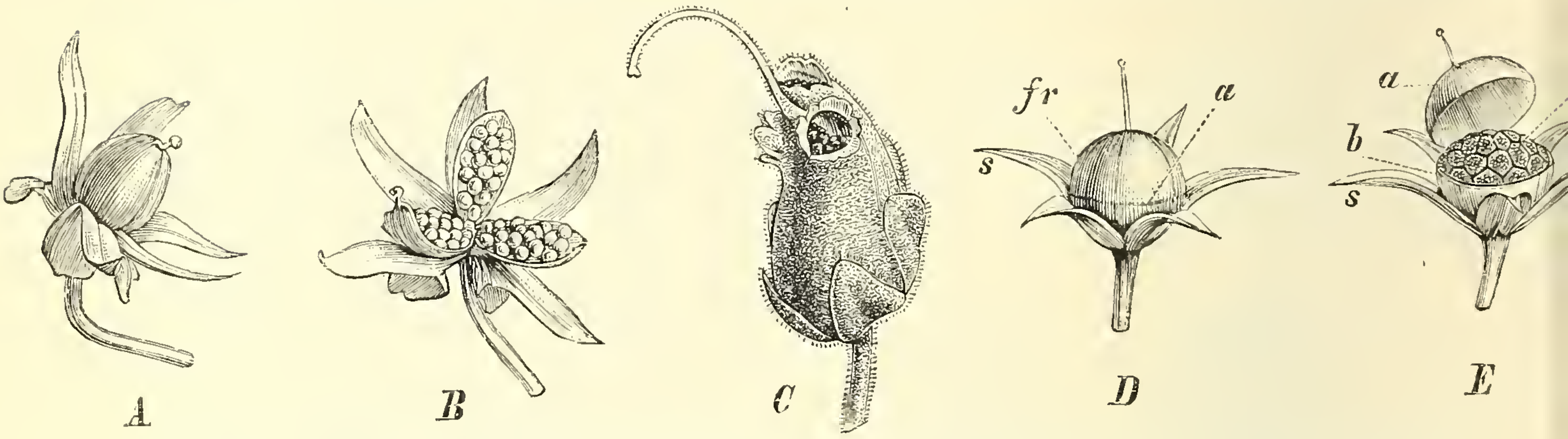


FIG. 407.—Modes of dehiscence of capsular fruits. *A*, *B*, *Viola tricolor* capsule before and after the dehiscence; *C*, porricidal capsule of *Antirrhinum majus* (magnified); *D*, *E*, pyxidium of *Anagallis arvensis* before and after dehiscence.

III. The Schizocarp is a dry, many-chambered fruit, in which the carpels separate from one another at maturity without dehiscing (*Umbelliferae*, *Malva*, *Galium*, Fig. 409).

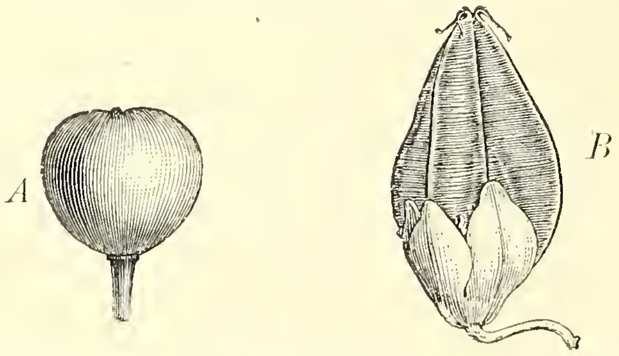


FIG. 408.—Dry indehiscent fruits. *A*, Nut of *Fumaria officinalis* (× 6); *B*, Achene of *Fagopyrum esculentum* (× 2). (After DUCHARTRE).

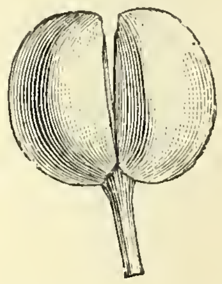


FIG. 409.—Schizocarp of *Galium mollugo*. (After DUCHARTRE, × 6).

IV. The Berry has both a juicy endocarp and mesocarp (Grape, Apple). In a few cases fruits of this type dehisce at maturity by slits (*Myristica*), or become irregularly ruptured (*Ecballium*).

V. The Stone-fruit or Drupe.—The pericarp is differentiated into a soft, generally juicy, exocarp and a hard endocarp (Cherry, Walnut). A single stone-fruit may contain several stones (*Rhamnus cathartica*). The exocarp is sometimes dry and spongy (Coco-nut).

The term spurious fruit may be applied to such cases as the Fig or Pine-apple, in which the inflorescence resembles a fruit. The Mulberry (Fig. 412, *B*), which is the inflorescence of a species of *Morus*, may be classed here also, more especially since it resembles so closely in general appearance the merocarpic fruit of species of *Rubus* (Fig. 412, *A*).

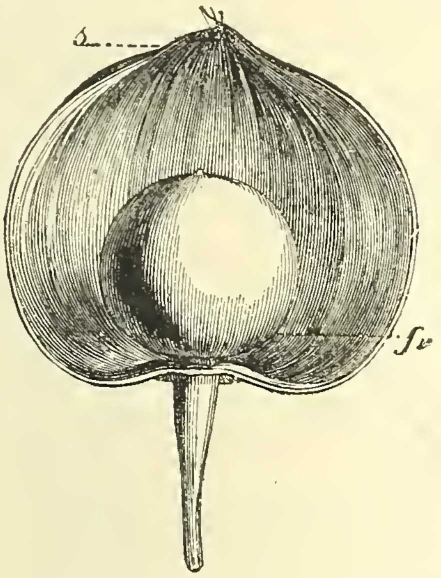


Fig. 410.—Fruit of *Physalis alkekengi*, consisting of the persistent calyx *s*, surrounding the berry *fr*, derived from the ovary. (After Duchartre.)

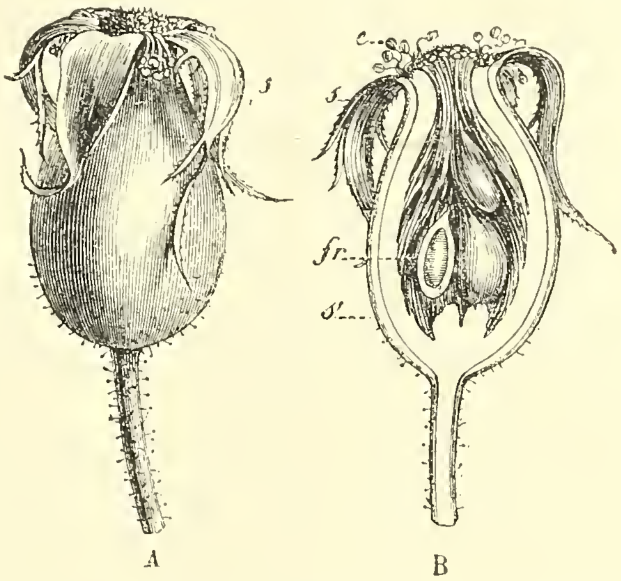


Fig. 411.—Fruit of *Rosa alba*, consisting of the fleshy hollowed axis *s'*, the persistent sepals *s*, and the carpels *fr*. The stamens *c* have withered. (After Duchartre.)

Just as the great variety of form displayed in flowers has been a result of their adaptation to a particular mode of pollination, so in fruits it has been intimately connected with the manner of seed dissemination (see Dissemination of Seeds, p. 288).

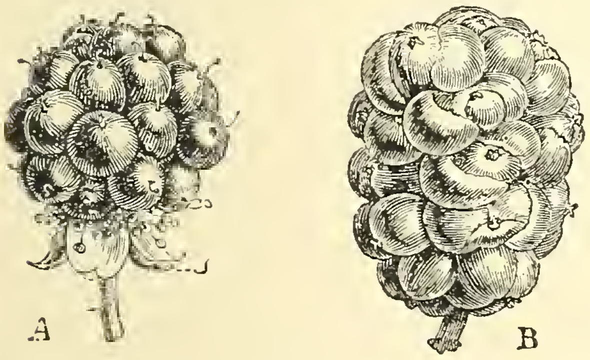


Fig. 412.—*A*, Merocarpic fruit of *Rubus fruticosus*, consisting of a number of drupes; *B*, inflorescence of Mulberry (*Morus nigra*) bearing a number of small drupes. (After Duchartre.)

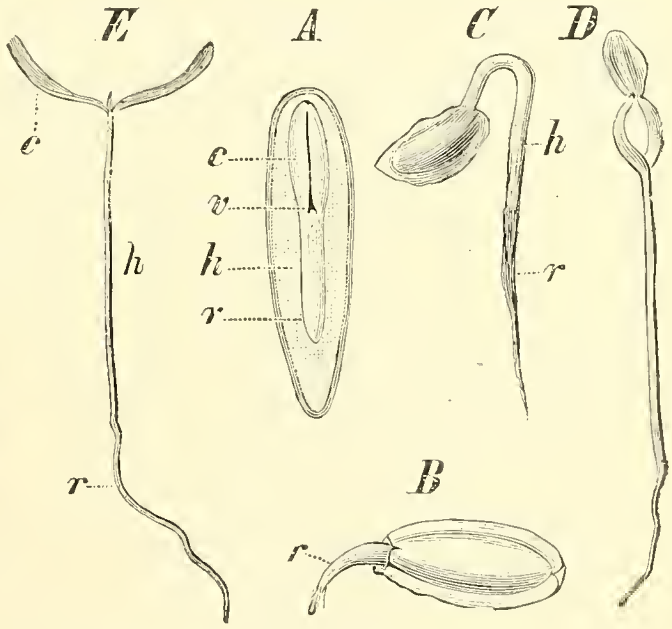


Fig. 413.—*Thuja occidentalis*. *A*, Seed in longitudinal section; *c*, cotyledons; *v*, plumule; *h*, hypocotyl; *r*, radicle: *B-E*, different stages of germination.

Germination.—The seed may either be liberated from the fruit as soon as it is ripe, or may never become free from it. The separation of the seeds in the Scotch Fir is effected very simply; the scales composing the cone separate a little from one another at maturity, so that the ripe seeds can fall out; in the Silver Fir, on the other hand, the scales separate from the axis of the cone and fall with the seeds. Seeds are also readily shed from the capsular fruits of many Angiosperms. From berries they are liberated by the agency of fruit-eating animals or by simple decomposition. The seeds are only slowly liberated by the decomposition of the pericarp enclosing them in indehiscent fruits or in drupes, or, and this is the more frequent case, the pericarp is thrown off on germination.

GERMINATION DEPENDS ON THE RESUMPTION OF ACTIVE LIFE BY THE DORMANT EMBRYO. The dry seed absorbs water and swells; the seed-coat is burst by the growth of the young plant. The root usually emerges first (Fig. 413) and, penetrating the soil, fixes the seedling and supplies it with the necessary water. After the nutritive material has been absorbed the cotyledons expand and turn green; the young plant is now capable of manufacturing food for itself. This, of course, only holds for autotrophic plants; parasites and saprophytes possess special adaptations to enable them to obtain their food-supply.

Table of the Classes and the most Important Orders and Families of Phanerogams

Class I. Gymnospermae

1. *Cycadinae.* Fam.: Cycadaceae.
2. *Ginkgoinae.* Fam.: Ginkgoaceae.
3. *Coniferae.* Fam.: Taxaceae, Pinaceae.
4. *Gnetinae.* Fam.: Gnetaceae.

Class II. Angiospermae

Sub-Class A. Monocotylae

1. *Liliiflorae.* Fam.: Juncaceae, Liliaceae, Amaryllidaceae, Iridaceae, Dioscoreaceae, Bromeliaceae.
2. *Spadiciflorae.* Fam.: Palmae, Araceae, Lemnaceae, Pandanaceae, Sparganiaceae.
3. *Glumiflorae.* Fam.: Cyperaceae, Gramineae.
4. *Helobiae.* Fam.: Hydrocharitaceae, Potamogetonaceae, Najadaceae.
5. *Scitamineae.* Fam.: Musaceae, Zingiberaceae, Cannaceae, Marantaceae.
6. *Gynandrae.* Fam.: Orchidaceae, Burmanniaceae.

Sub-Class B. Dicotylae

A. CHORIPETALAE

1. *Amentaceae.* Fam.: Salicaceae, Cupuliferae, Juglandaceae, Myricaceae, Casuarinaceae.

2. *Urticinae.* Fam. : Ulmaceae, Moraceae, Cannabinaceae, Urticaceae.
3. *Polygoninae.* Fam. : Piperaceae, Polygonaceae.
4. *Centrospermae.* Fam. : Chenopodiaceae, Amarantaceae, Caryophyllaceae.
5. *Polycarpicae.* Fam. : Ranunculaceae, Magnoliaceae, Myristicaceae, Menispermaceae, Berberidaceae, Lauraceae, Nymphaeaceae.
6. *Rhoeadinae.* Fam. : Cruciferae, Capparidaceae, Fumariaceae, Papaveraceae. Resedaceae.
7. *Cistiflorae.* Fam. : Cistaceae, Droseraceae, Violaceae, Hypericaceae, Clusiaceae, Ternstroemiaceae, Dipterocarpaceae.
8. *Passiflorinae.* Fam. : Passifloraceae, Begoniaceae.
9. *Opuntinae.* Fam. : Cactaceae.
10. *Columniferae.* Fam. : Tiliaceae, Sterculiaceae, Malvaceae.
11. *Gruinales.* Fam. : Geraniaceae, Oxalidaceae, Linaceae, Balsaminaceae, Erythroxylaceae, Polygalaceae.
12. *Terebinthinae.* Fam. : Rutaceae, Burseraceae, Zygophyllaceae, Simarubaceae. Anacardiaceae.
13. *Sapindinae.* Fam. : Aceraceae, Sapindaceae.
14. *Frangulinae.* Fam. : Celastraceae, Aquifoliaceae, Vitaceae, Rhamnaceae, Buxaceae, Empetraceae.
15. *Thymelaeinae.* Fam. : Thymelaeaceae, Elaeagnaceae.
16. *Tricoccae.* Fam. : Euphorbiaceae, Callitrichaceae.
17. *Umbelliflorae.* Fam. : Cornaceae, Araliaceae, Umbelliferae.
18. *Saxifraginae.* Fam. : Crassulaceae, Saxifragaceae, Platanaceae.
19. *Rosiflorae.* Fam. : Rosaceae.
20. *Leguminosae.* Fam. : Mimosaceae, Caesalpiniaceae, Papilionaceae.
21. *Myrtiflorae.* Fam. : Onagraceae, Haloragidaceae, Lythraceae, Punicaceae, Melastomataceae, Myrtaceae.
22. *Hysterophyta.* Fam. : Aristolochiaceae, Rafflesiaceae, Santalaceae, Loranthaceae.

B. SYMPETALAE

1. *Ericinae.* Fam. : Ericaceae, Pirolaceae.
2. *Diospyrinae.* Fam. : Sapotaceae, Styracaceae.
3. *Primulinae.* Fam. : Primulaceae, Plumbaginaceae.
4. *Contortae.* Fam. : Oleaceae, Loganiaceae, Gentianaceae, Apocynaceae, Asclepiadaceae.
5. *Tubiflorae.* Fam. : Convolvulaceae, Hydrophyllaceae, Cordiaceae, Boraginaceae.
6. *Personatae.* Fam. : Solanaceae, Scrophulariaceae, Utriculariaceae, Gesneraceae, Plantaginaceae.
7. *Labiatiflorae.* Fam. : Verbenaceae, Labiatae.
8. *Rubiinae.* Fam. : Rubiaceae, Caprifoliaceae, Valerianaceae.
9. *Campanulinae.* Fam. : Campanulaceae, Lobeliaceae, Cucurbitaceae.
10. *Aggregatae.* Fam. : Dipsacaceae, Calyceraceae, Compositae.

CLASS I

Gymnospermae ([19])

Flowers unisexual. Male flower, without perianth, consisting of scale-like stamens arranged spirally on an elongated axis. Pollen sacs 1-∞. Pollen conveyed to the micropyle of the ovule. The antheridium produced in the pollen-grain consists of one to three cells provided with cell walls. Carpels in *Cycas* grouped to form a flower at the summit of the axis, which continues its growth after flowering, so that the zones of carpels alternate with zones of vegetative leaves. Carpels in other cycads spirally arranged on the axis of a cone-like structure. Perianth absent. Carpels never united to form an ovary. In *Coniferae*, according to one interpretation, the bract scales are regarded as carpels, the ovuliferous scales as placental outgrowths from them; on this view each cone would be a single flower. According to another interpretation, the ovuliferous scales are regarded as axillary structures (cladode-like shoot, fused carpels borne by an axillary shoot, or a single carpel on an axillary shoot) in relation to the bract scale; on this view the cone would correspond to an inflorescence. The carpels of the *Coniferae* also are never united to form a closed ovary. Ovules exposed on the carpels, receiving the pollen into the micropyle. Prothallus filling the embryo-sac and bearing several archegonia. Fertilisation in *Cycadinae* and *Ginkgo* by means of spermatozoids, in other cases by non-motile sexual cells. Cotyledons two or more.

The Gymnosperms are woody plants, usually with needle-shaped, less commonly broader or pinnate leaves. Nervation of leaf usually very simple, sometimes parallel, rarely reticulate. Deviations from the type mainly among the *Gnetineae*.

Order 1. Cycadinae (20)

This order includes the single family **Cycadaceae**.—Flowers diœcious, WITHOUT A PERIANTH, consisting of many spirally-arranged leaves; staminal leaves with many pollen-sacs; carpellary leaves usually with two ovules. For the most part, UNBRANCHED, evergreen woody plants, devoid of true vessels and having MUCILAGE DUCTS in all organs. Leaves LARGE AND PINNATE (Fig. 414).

Many *Cycadaceae* resemble the Tree-Ferns not only in their column-like, unbranched stem and apical rosette of large, pinnate leaves, but also in their dimensions, attaining sometimes a height of 12 m.; in other cases the stems are shorter, resembling the *Marattiaceae* more in habit; they are tuberous and partially buried in the ground. The branching is limited to the flowering region, although sometimes adventitious shoots spring from the stem. In most species (*e.g. Cycas*) the stem is invested with a thick armour of woody scales, which are in part the basal portions of dead and fallen foliage-leaves, and in part scale-leaves (cataphylls), the development of which alternates periodically with that of the foliage-leaves.

The flowers of the *Cycadaceae* are always terminal; the stem, except in the female *Cycas* plants, is prolonged sympodially by a lateral branch, which crowds the flower to one side. The male flowers are cone-like, with numerous scale- or shield-shaped staminal leaves (Fig. 415), which bear an indefinite number of pollen-sacs on their under side. The species of *Cycas* produce a single, apical, female flower, of which the carpellary leaves are similar to the foliage-leaves, but on a reduced scale (Fig. 416). In other members of this family the apex of the stem terminates in several cone-like female flowers with scale-like leaves. Two or more ovules, larger than a cherry, are borne on each carpel. They are atropous, and provided at the apex of the

FIG. 414.—*Cycas revoluta*, female plant in flower. (From a photograph.)

nucellus with a cavity, the POLLEN-CHAMBER, in which the pollen-grains, which have been carried thither by the wind, accumulate preparatory to fertilisation. The *Cycads* that have been accurately investigated are found to possess spermatozoids (cf. p. 440). The seed resembles a drupe or stone-fruit in that the seed-coats are differentiated as an outer fleshy layer and a hard inner coat. The mealy endosperm envelops a two-leaved embryo attached to a coiled suspensor.

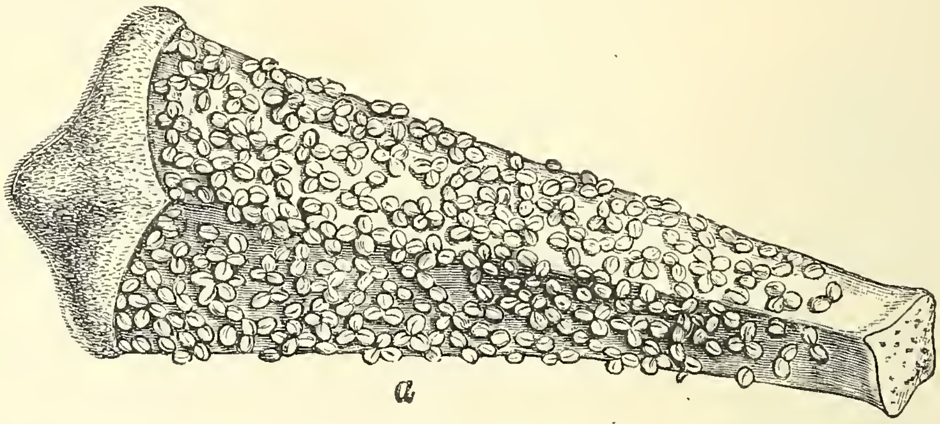


FIG. 415.—Stamen of *Cycas circinalis*, from below. (After EICHLER.)

FIG. 416.—Carpel of *Cycas revoluta*. (After EICHLER, reduced.

The *Cycadaceae* are all tropical or sub-tropical plants, and are found in both hemispheres, but with a limited area of distribution of the individual species. At the present time they occur only in small numbers; but in earlier geological periods up to the Cretaceous, as is proved by the extensive occurrence of fossil remains, they formed a considerable proportion of the vegetation of all zones.

Order 2. Ginkgoaceae (21)

Family **Ginkgoaceae.**—Female flowers long-stalked, usually with two ovules. FERTILISATION BY MEANS OF SPERMATOZOIDS. Seed-coat consisting of an outer fleshy and an inner hard layer. Leaves stalked, the lamina dichotomously divided (Fig. 417).

The *Ginkgoaceae* represent a very ancient branch of Gymnosperms which was well developed in earlier geological periods. The only existing representative is *Ginkgo biloba* (*Salisburya adiantifolia*), a deciduous tree occurring in China and Japan. It must be regarded as the type of a special order which has many points in common with the *Cycadaceae*.

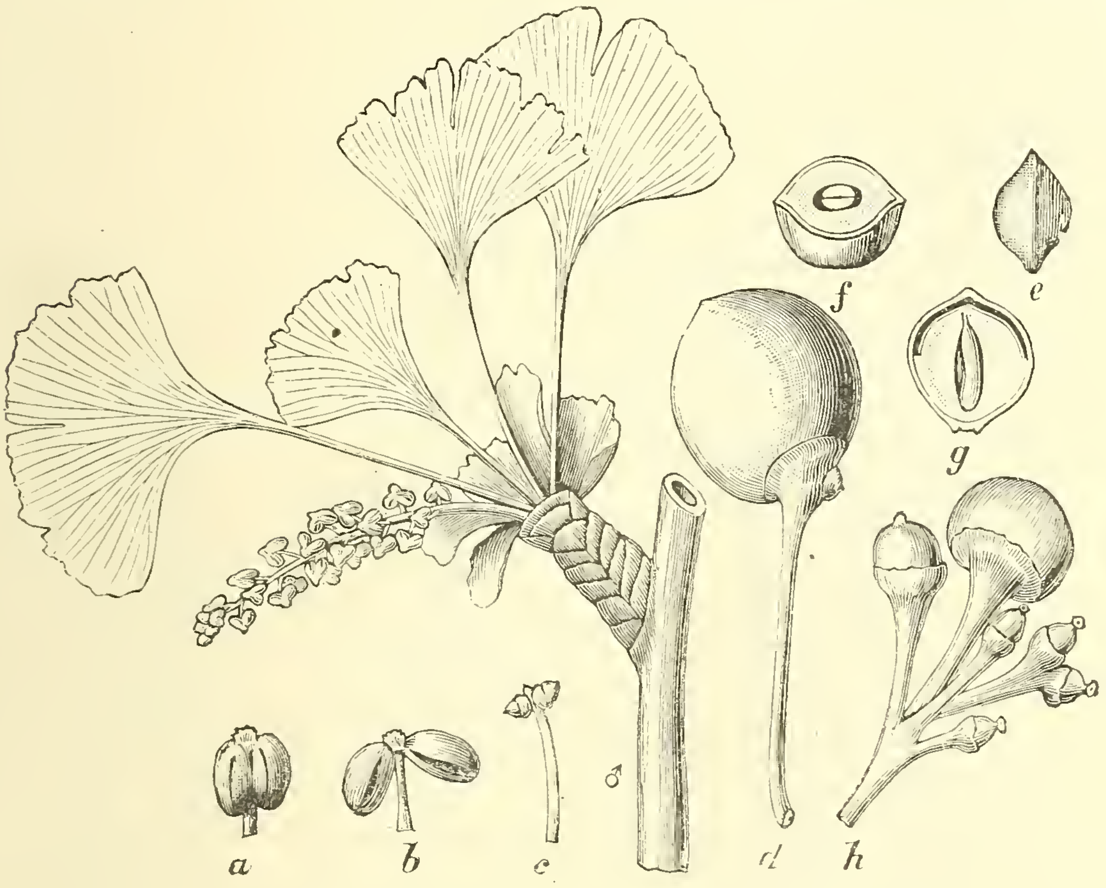


FIG. 417.—*Ginkgo biloba.* Male branch with flower; the leaves are not yet full grown. *a*, *b*, stamens; *c*, female flower; *d*, fruit; *e*, stone of same; *f*, stone in cross section; *g*, in longitudinal section showing the embryo; *h*, female flower with an exceptionally large number of ovules borne on separate stalks. (Male flower and *c* nat. size; *d*, slightly reduced; the other figures magnified. After EICHLER in *Natürl. Pflanzenfamilien.*)

Order 3. Coniferae (22)

Flowers NAKED; the male catkin-like with scale-like staminal leaves, bearing the pollen-sacs on the under side; the female flowers and the fruit of varying and sometimes complicated structure. What is here designated, for the sake of simplicity, a single female flower is also spoken of as an inflorescence. FREELY BRANCHING, woody plants DESTITUTE OF TRUE VESSELS, generally traversed in all parts by RESIN CANALS. Leaves simple, usually needle- or scale-shaped.

Many Conifers are tall forest trees of a pyramidal shape, with mast-like, tapering stems, from which spring apparent whorls of horizontal and much-branched lateral shoots. Frequently, when growing thickly crowded together, the lower branches fall off after a time, so that the stem becomes naked for the greater part of its height, and bears only a pyramid-shaped crown of upper branches. These may become finally more widely outspread, like the Mediterranean Pines (*Pinus Pinea*), or spread out horizontally, as in the Brazilian Araucarias (*Araucaria brasiliana*). Comparatively few of the arborescent species deviate from the pyramidal form; for example, the Cypress (*Cupressus sempervirens*), with its erect branches. The shrub-like species, such as the Junipers, on the contrary, are frequently irregularly branched and bushy.

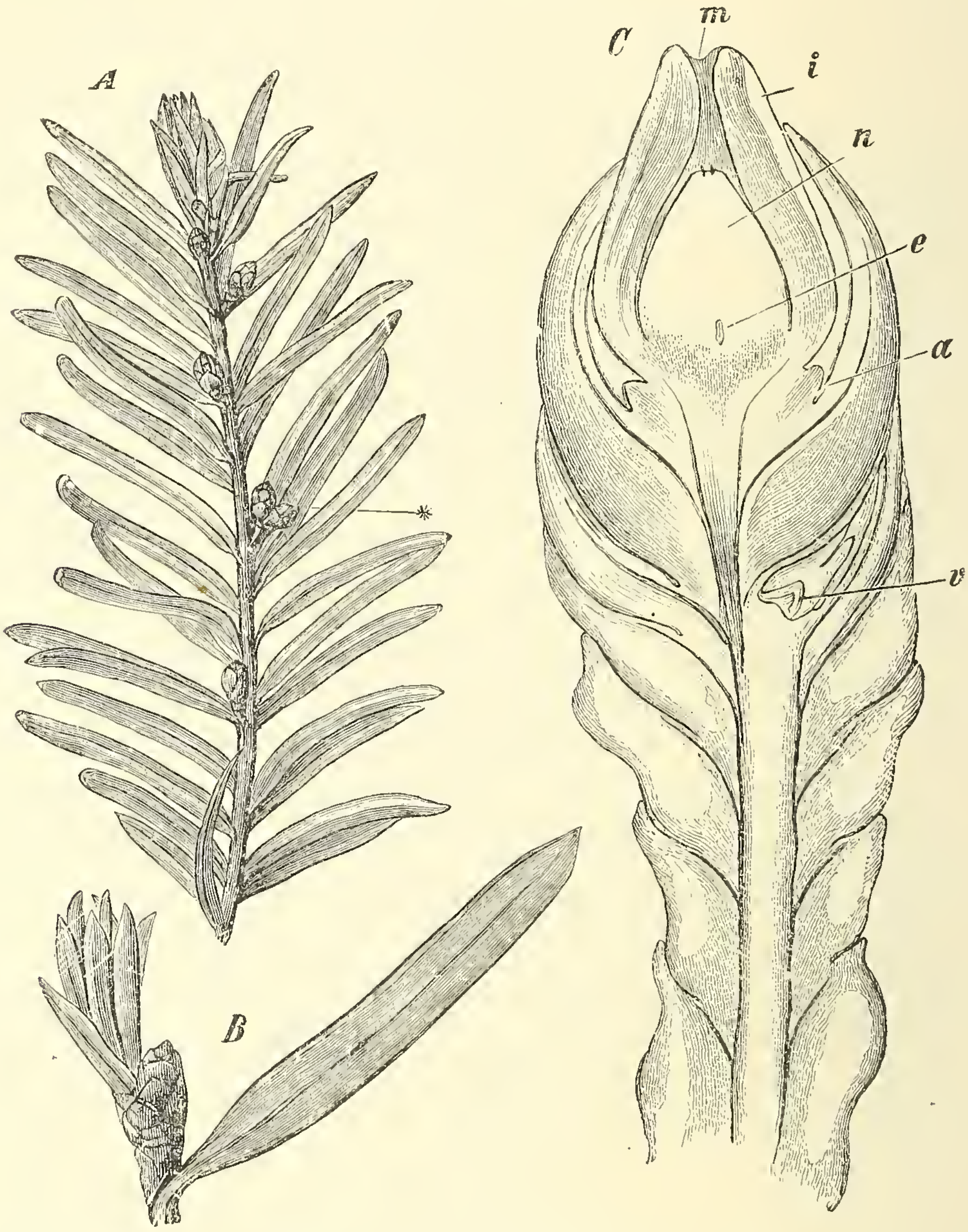


FIG. 418.—*Taxus baccata*. *A*, branch with female flowers: *, two ovules on the same shoot (nat. size); *B*, leaf with axillary, fertile shoot (× 2); *C*, median longitudinal section of a primary and secondary shoot; *v*, vegetative cone of the primary shoot; *a*, rudiments of the aril; *e*, rudiment of the embryo-sac; *n*, nucellus; *i*, integument; *m*, micropyle (× 48).—*POISONOUS*.

The male flowers are either solitary or aggregated in clusters; they fall after attaining maturity like the catkins of the Willow and other *Amentaceae*, which they also resemble somewhat in structure without morphologically being equivalent to them, since catkins are inflorescences. The stamens, which as a rule are numerous, are scale- or shield-shaped, with two or more, rarely many (as many as twenty in *Araucaria*), pollen-sacs on their under sides. The pollen-grains are frequently provided with two wing-like structures containing air.

The wide variations in the structure of the female flowers and the fruit constitute the distinctive characteristics of the different families into which the order is divided.

Family **Taxaceae.**—Formation of cones imperfect; the ripe seed possesses an aril.

Taxus baccata, the Yew (Figs. 418, 419), is an evergreen tree devoid of resin, sometimes attaining a height of 10 m. The shoots are all elongated and bear flat needles, arranged right and left, in two ranks. The male flower is axillary and consists of shield-shaped staminal leaves united in a spherical head surmounting the apex of a short stalk beset with scales below. The female flower also terminates the apex of a scaly, axillary stalk. The stalk, however, in this case is composed of a lower portion ending blindly, the primary shoot, and an upper lateral secondary shoot, which terminates in a single erect ovule. Carpels are wanting. The ripe seed is enclosed in a red cupular aril (Fig. 419).


FIG. 419.—*Taxus baccata*: branch with ripe seeds (½ nat. size).—POISONOUS.

GEOGRAPHICAL DISTRIBUTION.—The *Taxaceae* grow for the most part in the southern hemisphere and in Eastern Asia.

POISONOUS.—The young shoots and the seeds of *Taxus baccata*; the red enveloping aril, however, is harmless.

Family **Pinaceae.**—Female flowers, in the form of CONES; the ovules arising in scale-like carpels, and ripening to seeds while still enclosed in them; seed-coats dry, without an aril (Figs. 413, 420-425).

The male flowers (Figs. 420, 421) are capitate or cylindrical, frequently united in clusters. The female flowers consist generally of a spindle-shaped axis with numerous, spirally arranged, imbricated scales. In the Juniper and its allies the flower is composed of only a few verticillate carpels. In many genera the carpels are simple (*Juniperus, Agathis*); in others they have a scale-like outgrowth on the upper side; in other cases (Figs. 422, 423) again (*Abietoideae*), two scales are present, lying one above the other, the uppermost of which, the FERTILE SCALE, bears the ovules and is situated in the axil of the other, the cover-scale. The fertile scale is variously regarded as a placental outgrowth or a modified axillary shoot. Two ovules, less frequently only one or a larger number, spring from the basal portion of the fertile scale, on the upper side (Fig. 422); but in the *Cupressoideae* they are axillary, arising from a cushion-like swelling (Fig. 420).

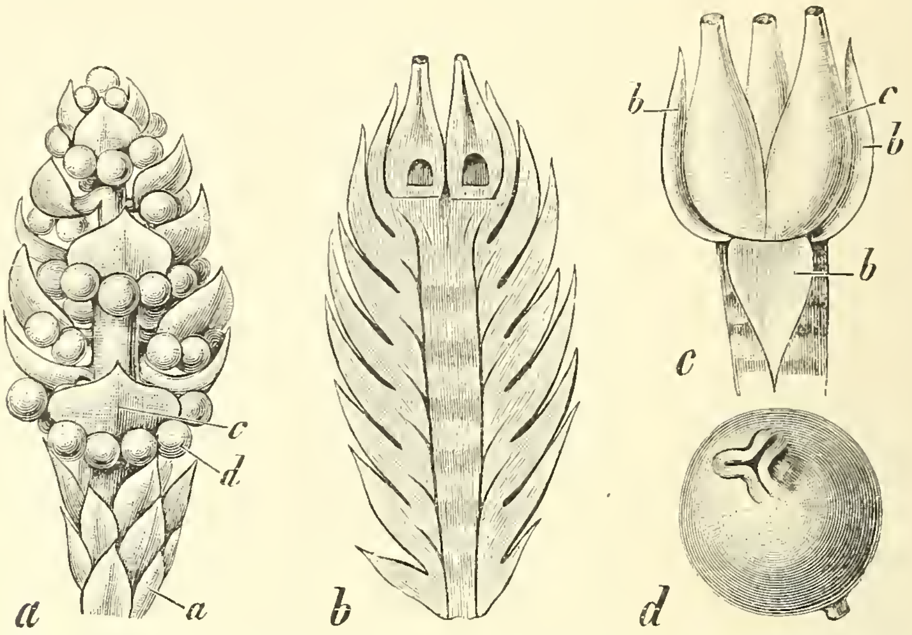


FIG. 420.—*Juniperus communis.* *a*, Male flower; *b*, fertile shoot with female flower; *c*, female flower with one scale bent out of place; *d*, fruit.—OFFICINAL. (After BERG and SCHMIDT, all magnified.)

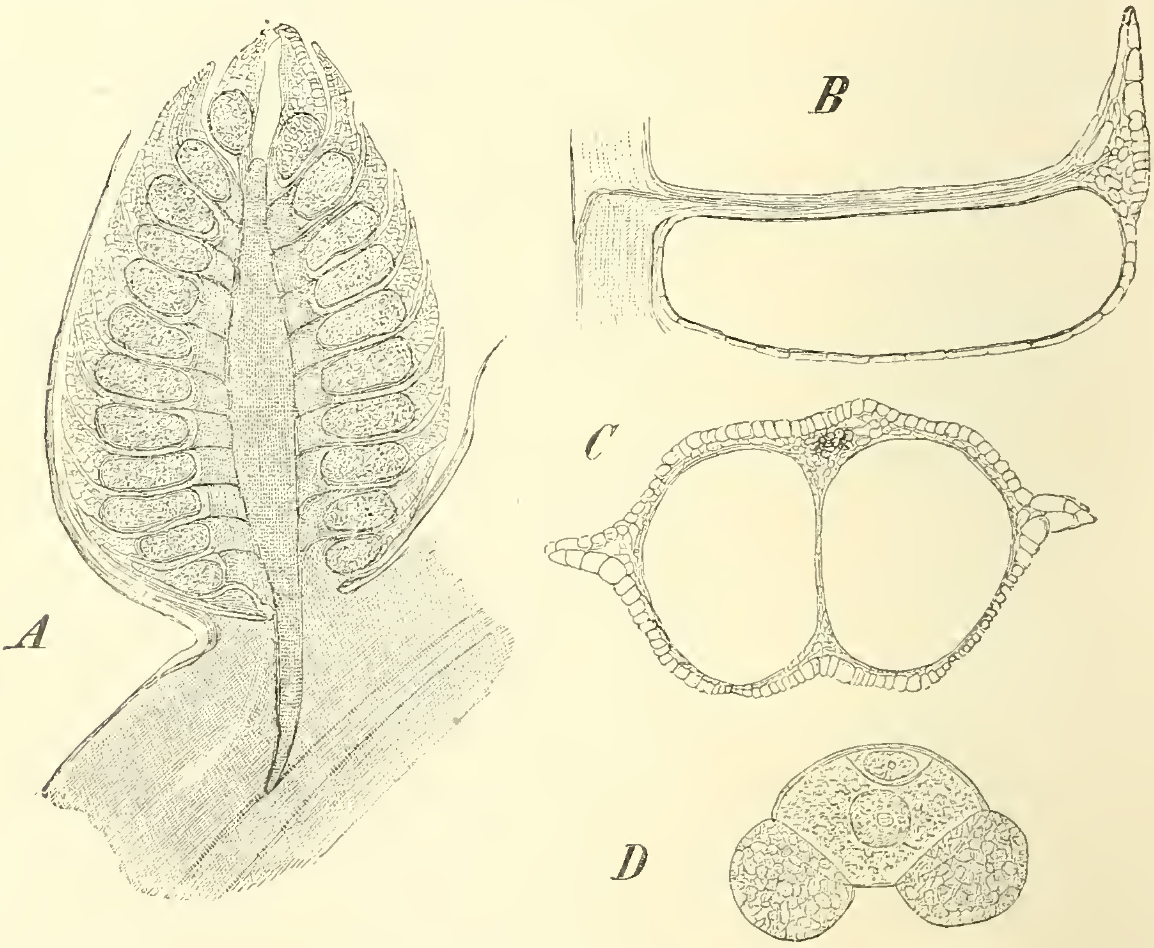


FIG. 421.—*Pinus Pumilio.* *A*, Longitudinal section of a ripe male flower (× 10). *B*, Longitudinal section of a single stamen (× 20). *C*, Transverse section of a stamen (× 27). *D*, A ripe pollen-grain of *Pinus silvestris* (× 400).

During the modification of the flower in the formation of the seeds, the scales in most cases become lignified, and the fruit, familiarly known as a cone, is thus produced. In some less frequent cases the fruit resembles a berry in form.

SUB-FAMILIES.—(1) *Cupressoideae.* Leaves opposite or in whorls; carpels simple; ovules axillary, erect. *Juniperus* (Juniper), *Cupressus* (Cypress), *Thuja* (Arbor Vitae). (2) *Taxodioideae: Taxodium* (American Cypress), *Sequoia.* (3) *Araucarioideae: Araucaria, Agathis.* (4) *Abietoideae.* Leaves spiral; carpels divided into cover- and fertile scale; ovules attached to the fertile scale, inverted. *Abies* (Silver Firs), *Picea* (Spruce Firs), *Larix* (Larches), *Pinus* (Pines).

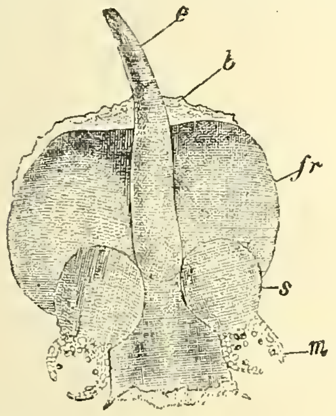


FIG. 422.—*Pinus silvestris.* Ovuliferous scale (*fr*) bearing two ovules *s* and the keel *c*. The bract scale *b* is visible behind. The free margin of the integument of the ovule forms two prolongations (*m*). (× 4.)

REPRESENTATIVE SPECIES.—*Juniperus communis* (Common Juniper, Fig. 420). Shrubs with needle-shaped leaves arranged in whorls of three, and having a resinous bloom; female flowers consisting of three scales, each with an axillary ovule; scales of the ripe fruit succulent and united, forming a berry. *Abies alba*, the Silver Fir (Fig. 423). Lofty forest trees upwards of 65 m. in height, with a silver-grey bark when old; crown pyramid-shaped, with horizontally extending, elongated branches: leaves needle-shaped, flattened on the under side, with two bluish-white longitudinal lines in addition to the middle nerve, displaced on the lateral branches in two comb-like rows on each side of the axis. The flowers are axillary and appear in May at the tips of the branches; the male flowers are cylindrical, some 20 mm. long, and bear numerous spirally-arranged staminal leaves, each having on the under side two pollen-sacs opening by a longitudinal slit (Fig. 423, *a*); the female flowers are oblong-cylindrical, about 6 cm. long, and consist of closely aggregated cover, and fertile scales arranged spirally on a spindle-shaped axis. The cones (*b*) are erect, their pointed cover-scales are much

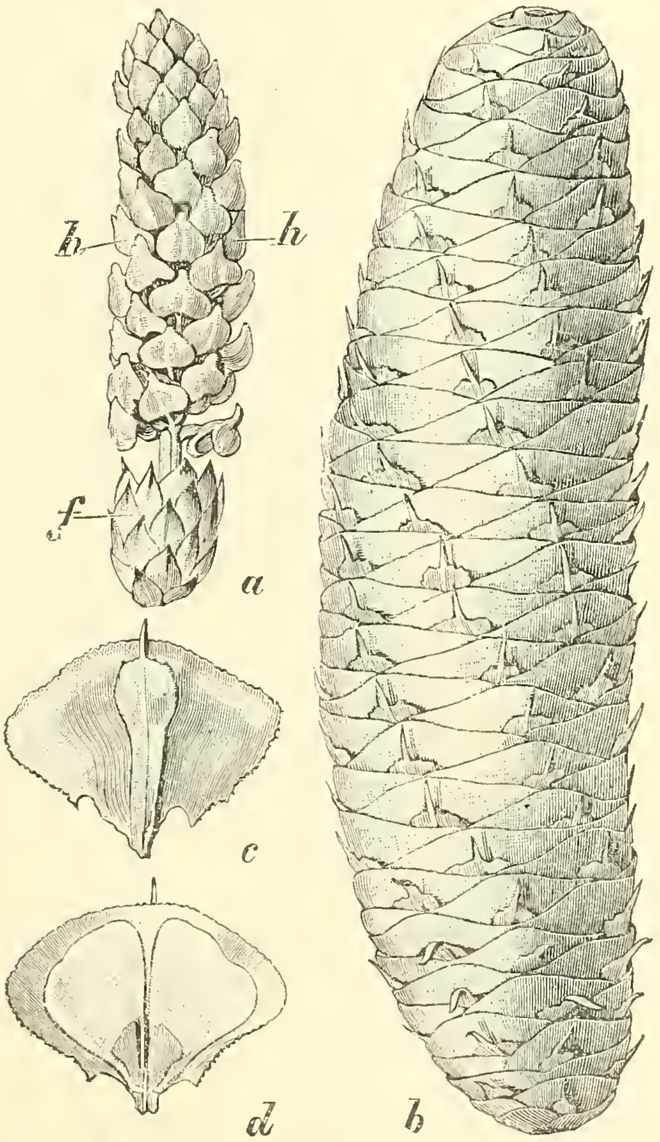


FIG. 423.—*Abies alba.* *a*, Male flower; *f* and *h*, sporophylls; *b*, cone; *c*, carpel, viewed from below (dorsal surface), showing the fertile and cover-scale; *d*, the same viewed from above (ventral surface). (After BERG and SCHMIDT; *a*, *c*, *d*, nat. size; *b*, reduced.)

narrower but longer than the fertile scales (*c*, *d*), and, in consequence, they are visible externally. At maturity the scales, together with the seeds (*c*, *d*), become detached from the axis and fall to the ground. *Picea excelsa*, the Norway Spruce, resembles the Silver Fir in size and appearance. The needles are four-sided, of a uniform colour, and point in all directions, but frequently bending to the right and left, appear as if arranged in comb-like rows. The cones are terminal and pendent; at maturity the seeds drop out and the cones then fall off entire, retaining their scales. The cover-scales are very small, and not visible externally. *Pinus silvestris*, the Scotch Fir, a forest tree upwards of 40 m. high with a dome-shaped crown. The needles are borne in pairs on greatly shortened lateral axes, or dwarf-shoots (spurs), provided with scale-like leaves. The male flowers (Fig. 424, 1, *a*), externally like those of *Abies*, spring closely crowded together from the summit of elongated shoots which, by continued growth, become prolonged beyond them, producing leafy dwarf-shoots. The female flowers are at first spherical and of a reddish colour (1, *b*). The cones (1, *c*) have very small cover-scales; but long woody fertile scales, thickened at the ends in rhombic areas, the apophyses. As in *Picea excelsa*, the cones fall off entire, after the seeds have fallen. *Larix europaea*, the European Larch, is particularly distinguished by its deciduous leaves, which are borne in clusters on short spurs.

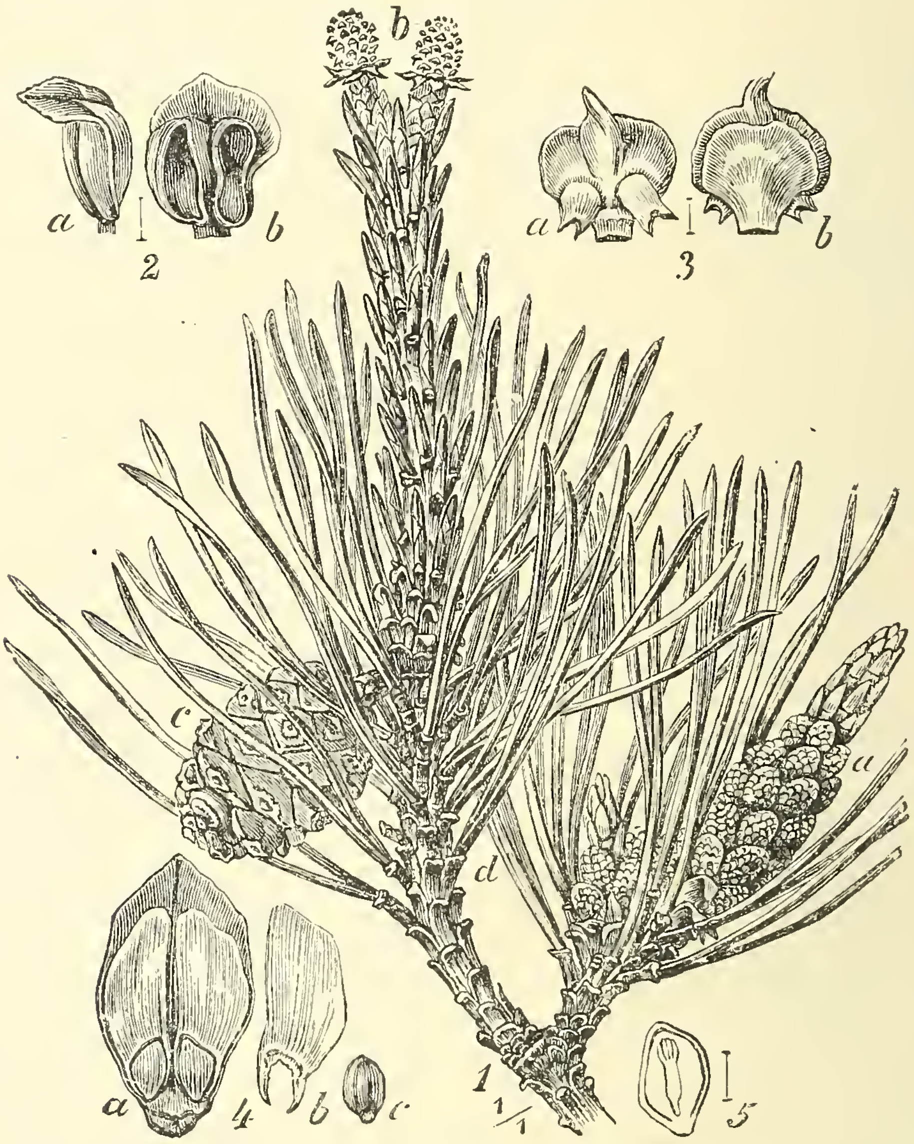


FIG. 424.—*Pinus silvestris.* 1, Branch with male (*a*) and female (*b*) inflorescences; *c*, cone; *d*, needles: 2, staminal leaf; *a*, viewed from the side; *b*, from below: 3, carpel; *a*, viewed from above; *b*, from below: 4, fertile scale with the two seeds (*a*), seed-wing (*b*), seed (*c*): 5, seed in longitudinal section.—OFFICINAL. (After WOSSIDLO.)

GEOGRAPHICAL DISTRIBUTION.—The *Pinaceae* inhabit chiefly the North Temperate Zone, where many species form by themselves widely extended forests. In countries bordering on the Northern Pacific, particularly in China, Japan, and California, they exhibit their most varied development. With the exception of the Australian *Eucalyptus*, the giant trees of California, *Sequoia gigantea*, with stems over 100 m. high and 12 m. in diameter, attain the greatest height of any trees in the world. Germany possesses only a few species of Conifers, some of which, however (*e.g. Pinus silvestris, Picea excelsa*), occur so abundantly that they constitute a large part of all the vegetation. The Silver Fir forms large woods in the Vosges and the Black Forest, but otherwise is rare. The common Juniper is also everywhere common on sandy soil. *Pinus montana*, *Pinus Cembra* (with three or five needles on each spur), *Larix europaea*, *Juniperus Sabina*, and *J. nana* are also found in Germany. They occur as trees and shrubs in mountainous regions.

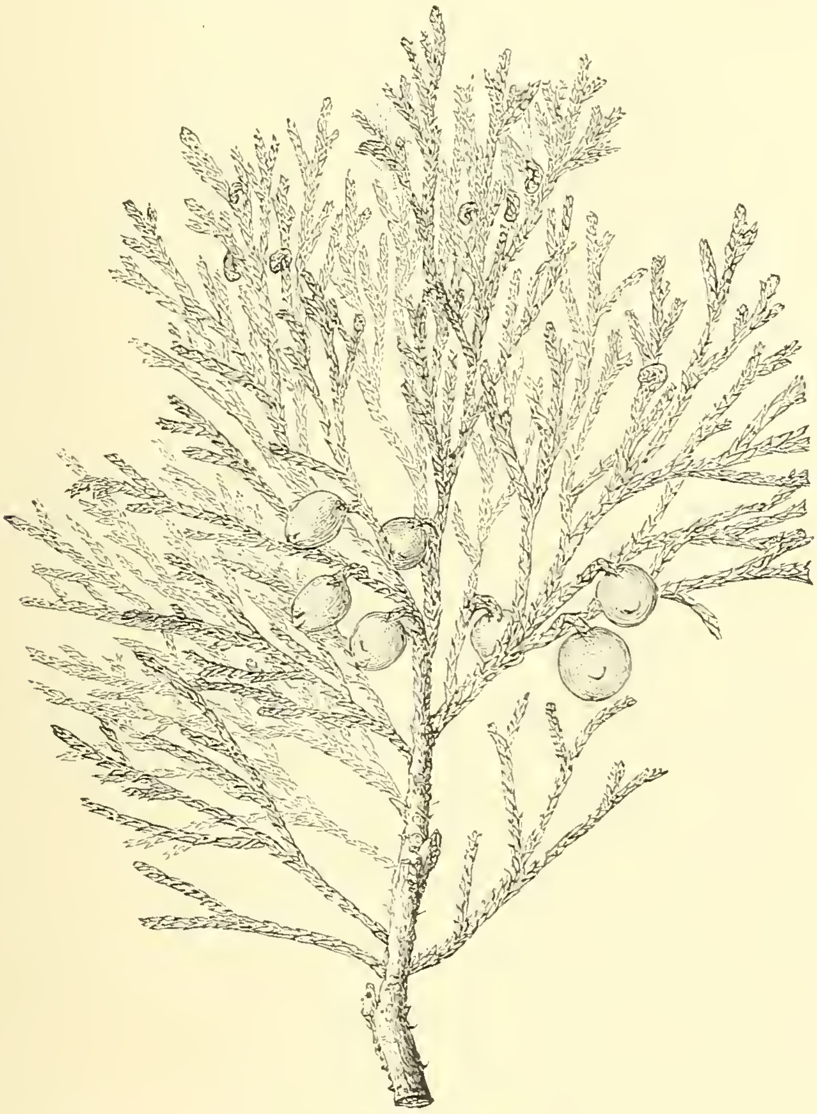


FIG. 425.—*Juniperus Sabina:* branch with fruit.—*OFFICINAL* and *POISONOUS.*

Many *Pinaceae* are cultivated in Germany on account of their beauty or economic value. In addition to the indigenous species, the following examples may be mentioned: *Pinus Strobus*, Weymouth Pine (North America); *Thuja occidentalis*, American Arbor Vitae; *Cedrus Libani*, Cedar of Lebanon; various species of *Araucaria*, from the temperate zone of the southern hemisphere.

POISONOUS.—*Juniperus Sabina*, a monœcious shrub with broom-like branching and scale, not needle-shaped, leaves. It grows wild in the Alps and is frequently cultivated in gardens (Fig. 425).

OFFICINAL.—*Juniperus communis*, FRUCTUS JUNIPERI, OLEUM JUNIPERI, and LIGNUM JUNIPERI; *Juniperus oxycedrus*, OLEUM CADINUM; *Juniperus Sabina*, HERBA OR SUMMITATES SABINAE; *Larix europaea*, TEREBINTHINA VENETA; *Larix sibirica* (North Russia, Siberia), PIX LIQUIDA. From different species of pines, as *P. silvestris*, *P. australis*, *P. Laricio*, *P. Pinaster*, *P. Taeda*, etc., and also from *Abies alba* and *Picea excelsa* are derived TEREBINTHINA, COLOPHONIUM, OL. TEREBINTHINAE, PIX LIQUIDA; from *Pinus Pumilio*, OL. PINI PUMILIONIS; *Pinus silvestris*, TURIO PINI.

Order 4. Gnetinae (23)

One family: **Gnetaceae.**—Flowers WITH PERIGONE; woody plants, without resin, and with TRUE VESSELS (Fig. 393).

In the presence of a perigone, which, however, is very small and insignificant; in the indication of a union of the sexes in an inflorescence in the case of *Gnetum*, and in the female flower of *Welwitschia*; in the possession of true vessels in the wood and sometimes of reticulately-veined leaves (*Gnetum*), the *Gnetaceae* show a resemblance to the Dicotyledons, and may accordingly be regarded as the most highly developed of all the Gymnosperms.

The three genera included in this family differ considerably from each other. The species of *Ephedra*, found in the Mediterranean region, are shrubby plants with slender branches devoid of foliage-leaves. The genus *Gnetum* (Tropical Asia and America) comprises trees and lianes with large reticulately-veined leaves. The only species of the third genus, *Welwitschia mirabilis* (South-west Africa), one of the most wonderful of all plants, has a thick, short, ovoid stem, which gives rise to only two band-shaped leaves over a metre long; as they continue to grow at the base, the leaves gradually die at the apex, and are torn into segments.

Fossil Gymnosperms (24)

In contrast to what was seen to be the case for the Pteridophyta, Gymnosperms have not yet been detected in Silurian strata. They appear first in the Devonian, where they are represented sparingly in North America. These earliest known remains are fragments of leaves referred to *Cordaites*. This genus belongs to a peculiar type confined to the Palæozoic rocks; it is the most ancient Phanerogam known. Owing to the excellence of the preservation of their remains the morphology of the *Cordaiteae* is as well known as that of the existing Gymnosperms. They were lofty trees with linear or broad and lobed leaves. Their flowers differ considerably from those of recent Gymnosperms. An important fact as bearing on the phylogeny of the group is the presence of a male prothallus as a small multicellular body. The ovules and seeds show great structural agreement with those of the *Cycadaceae*.

With the exception of some less common fossils (*Cycadites*, *Dicranophyllum*), the former of which is doubtfully referred to the *Cycadineae*, the latter more probably to the *Ginkgoineae*, *Cordaites* is the solitary, but richly represented, type of Gymnosperm found in the Carboniferous rocks. Undoubted *Cycadaceae* make their appearance in the lower Rothliegende. In later strata the genus *Walchia*, of uncertain affinity, appears; the vegetative organs, which alone are known, recall the lowest *Coniferae* (*Araucariaceae.*) In the upper Rothliegende undoubted *Ginkgoaceae* (*Baiera*) make their appearance, with another type referred to the *Coniferae* (*Ullmannia*).

The Cordaiteae disappear in the Rothliegende. The Gymnosperm flora can be followed through the Trias, in which it consisted of extinct types of *Cycadineae*, *Ginkgoineae*, and *Coniferae* (*Voltzia*, which apparently belonged to the *Taxodieae*, in the Bunter Sandstone), to the Jurassic period. In the latter it attained a great development in that both the *Ginkgoineae* and the *Cycadineae* attained their maximum development and were represented by numerous forms. True *Araucarieae* also appear in the Jurassic ; on this account, as well as on account of their organisation, this group may be regarded as the oldest of the existing Coniferae.

In the Wealden, *Cycadineae* and *Ginkgoineae*, along with some *Coniferae*, were dominant among the Gymnosperms. On passing to the Cretaceous strata the ancient types are found to be reduced, while the *Coniferae* become more numerous. Among the latter existing genera appear (*Dammara*, *Sequoia*, *Pinus*, *Cedrus*, *Abies*, *Callitris*, etc.) The *Taxaceae* also appear to be represented, but the remains are of uncertain affinity.

The Tertiary Gymnosperms belong entirely to existing types and for the most part to existing species. The *Coniferae* are dominant ; the *Ginkgoineae* are represented only by *Ginkgo biloba*, but this occurred in Europe along with other species now limited to Eastern Asia or North America (*Cryptomeria japonica*, *Taxodium distichum*, *T. heterophyllum*, *Sequoia gigantea*, *S. sempervirens*, *Pinus Strobus*, etc.). One Cycadaceous plant (*Encephalartos*) is also known.

CLASS II

Angiospermae

Flower with its parts arranged in whorls, with shortened axis, mostly with calyx and corolla, hermaphrodite or unisexual by abortion. Stamens consisting of filament and anther, the latter containing four pollen-sacs in the two thecæ. Antheridium reduced to a single naked cell. Carpels usually united to form the ovary, within which the ovules are contained ; less commonly the carpels are free, each uniting by its margins to form an ovary. The upper parts of the carpels are free or coherent, forming the style or styles which bear the stigmas, *i.e.* the region destined to receive the pollen. In the embryo-sac previous to fertilisation two groups of three cells originating by successive divisions come to occupy the two poles ; the group at the micropylar end is the egg-apparatus, that at the opposite end consists of the antipodal cells. There is a naked ovum in the egg-apparatus. This is fertilised by one of the naked male generative cells in the pollen-tube. The other generative nucleus fuses with the nucleus of the embryo-sac, which then by repeated division gives rise to the endosperm. Cotyledons one or two. Herbs and woody plants of very various form. Leaves parallel-veined or net-veined.

SUB-CLASS I

Monocotyledones (1, 2)

Flowers constructed for the most part after the TRIMEROUS, pentacyclic type; seeds usually abundantly provided with nutritive tissue; embryo with ONE cotyledon. Herbs and woody plants with CLOSED and usually scattered vascular bundles (Fig. 426), nearly always WITHOUT CAMBIUM; when a cambium is present, it lies outside the vascular bundles. Leaves commonly with PARALLEL nervation.

The embryo, in the majority of Monocotyledons, is small in comparison with the albumen (endosperm, rarely perisperm). It consists, as a rule, of a short hypocotyl, with a still shorter root and a relatively large cotyledon, which on germination remains wholly or in part enclosed within the seed, and exhausts the albumen of its food material.

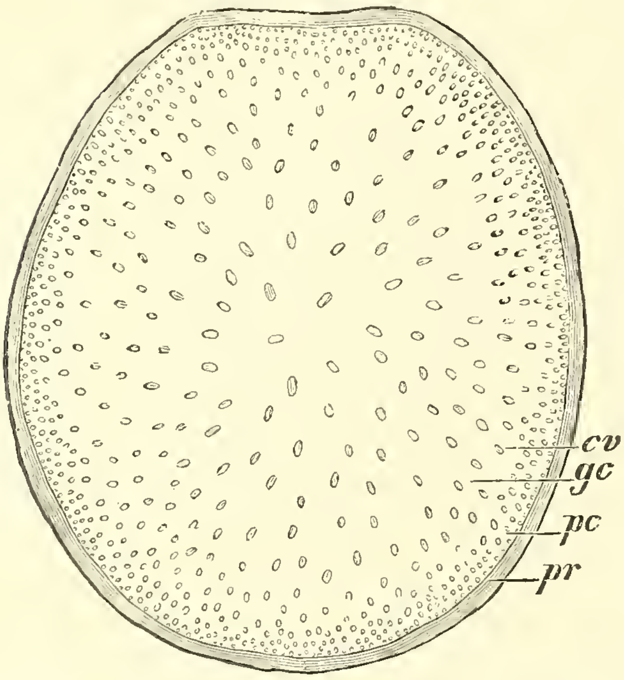


FIG. 426.—Transverse section of the stem of *Zea Mais*. *cv*, Vascular bundle. (For further description see p. 106 and Fig. 120.)

The primary root dies prematurely and is replaced by adventitious roots, which usually live but a short time, and are in turn superseded by others developing successively higher and higher on the stem. The roots are generally unbranched, and exhibit secondary growth in thickness only in the few cases when a cambium is present in the stem.

The stem of most Monocotyledons is simple; when branching does occur, it rarely results in the formation of a profusely-branched crown. (With respect to the disposition and structure of the vascular bundles of the stem, see pp. 106, 112; for occurrence and description of secondary growth, p. 138). The leaves are always devoid of stipules, and, in the majority of cases, alternate, arranged in two or three ranks. They generally have a well-developed sheathing leaf-base, are without stalks, and are lineal or elliptical in shape and parallel-nerved (Fig. 427), although leaves otherwise constructed not infrequently occur.

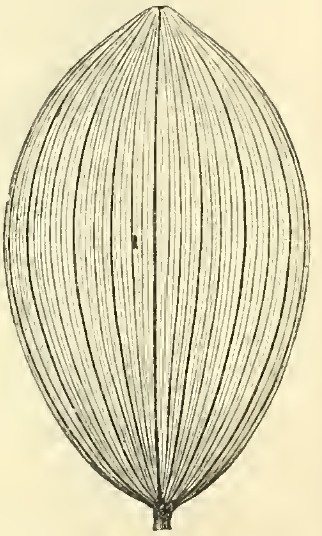


FIG. 427.—*Polygonatum multiflorum*, leaf with parallel venation. (Nat. size.)

The structure of Monocotyledonous flowers may be traced back, in almost every case, to the trimerous pentacyclic type (Fig. 428). It may accordingly be inferred that the flower of the ancestral form was actinomorphic, and composed of five alternating trimerous whorls, each whorl consisting of similar members.

This type has been retained unchanged in many Monocotyledons; in others, modifications have occurred in the course of their phylogenetic development, resulting sometimes in a transition from an actinomorphic to a zygomorphic or asymmetrical structure, sometimes in a reduction in the number of members in the whorls, less frequently in an increase. The more important of these deviations from the usual type will be noticed in detail in the descriptions of the single families.

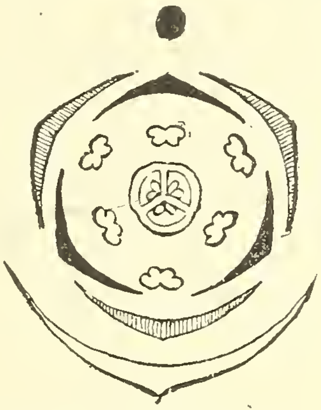


Fig. 428.—Diagram of a typical Monocotyledonous flower.

The perianth is not usually differentiated into a calyx and corolla; it is small and inconspicuous or large and highly coloured according to the mode of pollination, whether effected by the wind or insects. In a few cases of entomophilous pollination the perianth remains insignificant, and other parts of the plant assume the function of an attractive apparatus (cf. *Araceae*).

The Monocotyledons are divided into the following orders: *Liliiflorae*, *Enantioblastae*, *Spadicieiflorae*, *Glumiflorae*, *Helobiae*, *Scitamineae*, *Gynandrae*. These orders do not constitute a continuous series, beginning with the most primitive forms and successively ascending to those more highly developed, but represent rather a group of isolated branches, of which the common stock has become extinct.

The *Scitamineae* and *Gynandrae*, the most highly developed of the Monocotyledons, have probably arisen, however, from the *Liliiflorae*. Many things seem to indicate that the primitive Monocotyledons were grass-like and adapted to wind-pollination; in particular, the circumstance that the simplest representatives of several of the orders possess such a form, while the orders *Scitamineae* and *Gynandrae*, in which this is not the case, are manifestly of later origin.

Order 1. Liliiflorae

Type.—Flower hypo- or epigynous, ACTINOMORPHIC, rarely slightly zygomorphic, always with a PERIANTH consisting of complete, fully-developed whorls: P 3 + 3, A 3 + 3 or A 3, G (3). Ovary three-locular. Ovules anatropous or campylotropous, rarely atropous. Endosperm always present, enclosing the embryo.

In the majority of the *Liliiflorae*, the flowers exhibit the typical Monocotyledonous form (Fig. 428), and are actinomorphic, with five trimerous whorls, the members of each whorl being similar. The slight zygomorphism displayed by some of the forms is occasioned by the one-sided curvature of the stamens. The only essential deviation from the Monocotyledonous type is restricted to a few families, and consists in the suppression of a whorl of the andrœcium. The suppression of single members of the whorls does not occur.

In some genera the whorls are composed, instead of three, of two, four, or five members. These variations are due neither to reduction nor to splitting, and are attributable to differences existing in the very rudiments of the organs. The number of members in the whorls may vary even in the same species, *e.g.* in *Paris quadrifolia*, which, in addition to the usual tetramerous flowers, not unfrequently produces others constructed on the plan of five or six.

The *Liliiflorae* are, with few exceptions, herbs, in which the subterranean parts often take the form of perennial rhizomes or bulbs, while the aerial shoots usually die after the ripening of the seeds. In only the simplest, apparently oldest, grass-like forms are the flowers inconspicuous and adapted to wind-pollination; otherwise they are large, beautifully coloured, solitary or aggregated into loose inflorescences.

The differences between the families are not uniformly constant; on the contrary, in some of the species of almost every family, characteristics distinctive of other families occur, *e.g.* three stamens in families in which six is the normal number. Similarly, in nearly every family transitional forms are found which link the different alliances together.

Of all the families of the *Liliiflorae*, the *Juncaceae* probably resemble most clearly the primitive type. From primitive forms, similar to this family, have arisen on the one side the *Liliaceae* (some of the representatives of which still possess a grass-like character), and on the other side the *Glumiflorae*. Most of the other *Liliiflorae*, *e.g.* the *Amaryllidaceae* and *Iridaceae*, are probably descended from the *Liliaceae*, as well as the orders *Gynandrae* and *Scitamineae*, but in these metamorphosis and reduction have advanced further.

FIG. 429.—*Juncus lamprocarpus*. *a*, Part of an inflorescence; single flower (*b*) and gynœcium (*c*) more highly magnified.

Family **Juncaceae**.—Flowers hypogynous, hermaphrodite, with GLUMACEOUS perigone; pollen in tetrads; ovary uni- or tri-locular; three long papillose stigmas, endosperm mealy; GRASS-LIKE plants (Fig. 429).

The *Juncaceae* in the structure of their flowers agree essentially with the *Liliaceae*, their points of disagreement being for the most part due to their different mode of pollination. In the *Juncaceae* pollination is effected by the wind; their flowers are correspondingly inconspicuous and provided with dry pollen and large papillose stigmas. The inflorescences are variously constructed. The fruit is a capsule. In the genus *Juncus* (Bog-Rush) the capsules are many-seeded; in *Luzula* (Wood-Rush), three-seeded.

GEOGRAPHICAL DISTRIBUTION.—The *Juncaceae* grow in the temperate and cooler zones of both hemispheres.

Family **Liliaceae.**—Flowers HYPOGYNOUS; perigone COROLLACEOUS; six stamens; seed with endosperm, which is either oily or consists largely of cellulose (Figs. 430-435).

FIG. 430.—*a-e*, *Ornithogalum umbellatum*; *a*, entire plant (reduced); *b*, flower (nat. size); *c*, flower, part of perigone and andrœcium removed; *d*, fruit; *e*, fruit in transverse section; *f-g*, *Colchicum autumnale*; *f*, fruit in transverse section; *g*, section through seed showing endosperm (*e*). (*c-g* magnified.)

Most of the *Liliaceae* are succulent herbs with perennial bulbs or rhizomes; the species of *Aloe* and *Dracaena*, however, are in part shrubs or small trees (Figs. 433, 434). The leaves are not segmented into stalk and lamina, and are usually narrow in proportion to their length, undivided and rarely toothed (*e.g.* some species of Aloe). The flowers, which are often large and conspicuous, are solitary and terminal, as in the Tulip, or are aggregated in racemes, like the Hyacinth, less frequently in profusely-branched and complicated inflorescences. They are adapted to insect-pollination and are provided with means of enticement, such as white or highly-coloured perigone leaves, sweet perfume, nectaries, etc. The fruit is a capsule or berry.

Fig. 431.—*Colchicum autumnale*. *a*, Flowering plant (¾ nat. size); *b*, leafy shoot with fruit (½ nat. size). —*Poisonous* and *Officinal*.

Fig. 432.—*Paris quadrifolia* (⅗ nat. size).—*Poisonous*.

Sub-Families and Representative Genera.—(1) *Melanthoideae*. Three styles, septicidal capsules; *Veratrum; Colchicum; Sabadilla*. (2) *Lilioideae*. One style, loculicidal capsules; *Tulipa, Lilium; Hyacinthus; Muscari; Ornithogalum* (Fig. 430); *Scilla; Urginea; Allium*, bulbous plants with radical leaves and compound bostrychoid inflorescences; *Aloe*. (3)

Asparagoideae, without bulbs; fruit a berry; *Polygonatum; Majanthemum,* with dimerous flower; *Convallaria; Paris; Asparagus,* with needle-shaped, leafless branches; *Smilax; Dracaena,* dichotomously branching trees with secondary growth (Figs. 434, 155).

Geographical Distribution.—Members of the large family *Liliaceae* are found widely distributed in all zones, yet a preference seems to be shown for the dry warmer parts of the temperate Zone. Numerous species are found in fields and meadows of the Mediterranean countries. Members of this family occur in profusion in South Africa, where during the short spring, in company with other bulbous and tuberous plants (*Iridaceae, Amaryllidaceae, Orchidaceae*), they cover the earth with a carpet of purple, red, yellow and orange flowers only to disappear on the first approach of the dry season, the underground portions alone remaining alive. Many *Liliaceae* are cultivated as vegetables—*Asparagus officinalis,* asparagus; *Allium Cepa,* onion; *A. sativum,* English garlic; *A. Schoenoprasum,* chives; *A. ascalonicum,* shallots. Other *Liliaceae* are familiar as ornamental plants: the various species of Tulip, Hyacinths, Lilium, Scilla, Fritillaria, Yucca, Dracaena, Aloe, etc.

Poisonous.—*Colchicum autumnale,* Meadow Saffron (Fig. 431). It possesses a subterranean tuber, which gives rise to the rose-coloured, funnel-shaped flowers in August or September, followed in the succeeding spring by the leaves and fruit; at other seasons of the year the plant exists only in the form of a tuber. The fruit is a trilocular, many-seeded capsule. The whole plant, particularly the tubers and seeds, contains a large percentage of the poisonous alkaloid colchicin. *Veratrum album* is a profusely leaved, tall herb growing in meadows in mountainous regions, with a fleshy, perennial rhizome; the numerous green, choripetalous flowers are aggregated into a terminal, pyramid-shaped panicle. The poisonous properties of the plant are due to the presence of veratroidin and jervin. *Paris quadrifolia,* Herb Paris (Fig. 432), is an herb with a single whorl of four leaves. Each plant produces one terminal tetramerous flower of a greenish colour, from which the fruit, a black berry, develops. The toxic principle in this case is paridin. The Lily of the Valley (*Convallaria majalis*), the bulbs of the Tulip (*Tulipa*) and of the Crown Imperial (*Fritillaria imperialis*) are also more or less poisonous.

Fig. 433.—*Aloe socotrina.* 1, Entire plant (reduced); 2, a flower.—*Officinal.* (After Wossidlo.)

Officinal.—*Colchicum autumnale* yields Semen Colchici; *Veratrum album,* Rhizoma Veratri; *Sabadilla officinarum* (grass-like, small-leaved bulbous plants of Central America and Venezuela).

SEMEN SABADILLAE and VERATRINUM. ALOE is derived from the evaporated sap of the leaves of South African species of *Aloe* (herbs, shrubs, or small trees with fleshy, often serrate leaves ; inflorescence a loose raceme with leafless or scaly axis ; perigone leaves united into a tube, Fig. 433). *Urginea maritima* (Mediterranean bulbous plants with leafy stalk, terminating in a raceme of white flowers) yields BULBUS SCILLAE (*Squill*). RADIX SARSAPARILLAE is procured from Central American species of *Smilax* (for the most part prickly plants climbing by tendrils ; flowers diœcious, greenish : ovules atropous). *Convallaria majalis ;* HERBA CONVALLARIEAE.

FIG. 434.—*Dracaena draco.* The Dragon tree of Laguna in the Canary Islands. (From CHUN, *Aus den Tiefen des Weltmeeres.*)

Family **Amaryllidaceae**.—As in the *Liliaceae,* except that the flowers are EPIGYNOUS (Fig. 436).

Herbs, usually bulbous ; very similar to the *Liliaceae* in appearance and mode of life.

REPRESENTATIVE GENERA.—*Narcissus*, with a corona or inner corolla : *Galanthus ; Leucojum ; Agave,* resembling the Aloe in appearance.

GEOGRAPHICAL DISTRIBUTION.—The same as the *Liliaceae.* The *Agave Americana* from Mexico has grown wild in the neighbourhood of the Mediterranean, and has now become a characteristic plant of that region. *Galanthus nivalis,* Snowdrop ; *Leucojum vernum,* Snowflake ; *Narcissus poeticus* and *N. pseudonarcissus.* etc., are familiar cultivated plants.

Family **Iridaceae**.—The INNER CIRCLE OF STAMENS IS SUPPRESSED, otherwise similar to the *Amaryllidaceae* (Figs. 437, 439).

The *Iridaceae* are herbaceous plants with rhizomes, rarely with

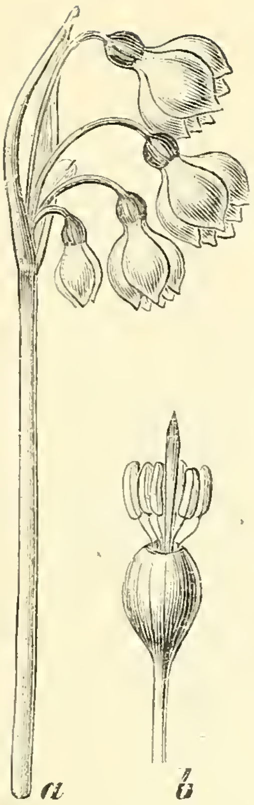


FIG. 436.—*Leucojum aestivum.* *a*, Inflorescence (reduced); *b*, gynœcium and andrœcium (nat. size).

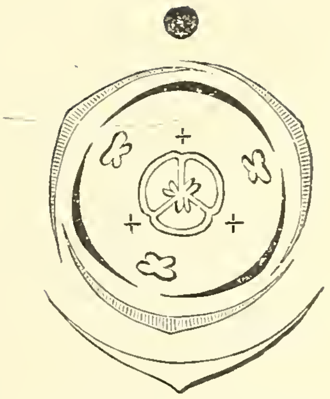


FIG. 437.—Floral diagram of the *Iridaceae* (*Iris*).

FIG. 435.—*Urginea maritima* (reduced.) OFFICINAL. (After BERG and SCHMIDT.)

FIG. 438.—*Iris florentina.* *A*, Rhizome with stem and leaves (reduced); *B*, inflorescence (reduced); *C*, stigmatic branch and stamen; *D*, ovary in longitudinal section; *E*, ovary in transverse section.—*OFFICINAL.*

bulbs; they are very similar to the two preceding families, but frequently have narrow, two-ranked, equitant leaves. The flowers are usually large and showy; the fruit is a loculicidal capsule.

FIG. 439.—*Crocus sativus.* Style with tripartite stigma. *OFFICINAL.* (After BAILLON.)

REPRESENTATIVE GENERA.—*Iris*, with rhizome, and equitant, sword-shaped leaves and petaloid stigmas; *Crocus*, with tuberous rhizome, and linear leaves (not equitant); *Gladiolus*, with zygomorphic flowers.

GEOGRAPHICAL DISTRIBUTION.—Like the *Liliaceae*, the *Iridaceae* are particularly abundant in Southern Africa. Various species of *Iris*, *Crocus*, *Gladiolus* are cultivated as ornamental plants.

OFFICINAL.—*Iris germanica*, *I. pallida*, and *I. florentina* (Fig. 438), all Mediterranean species, supply Orris Root, RHIZOMA IRIDIS. The stigmas of *Crocus sativus* (Fig. 439) (cultivated in different localities, derived from the East) yield Saffron or CROCUS.

Family **Dioscoreaceae.**—Climbing plants related to the *Amaryllidaceae*. *Tamus communis*, in Central Europe.

Family **Bromeliaceae.**—In Tropical America. Pine-apple is the inflorescence of *Ananassa sativa*.

Order 2. Spadiciflorae

Flowers hypogynous, usually DICLINOUS, actinomorphic, frequently REDUCED. Inflorescence, a SPADIX OR COMPOUND SPIKE, WITH ONE OR MORE SPATHES (large sheathing bracts) at the base.

The *Spadiciflorae* comprise herbaceous and woody plants of dissimilar appearance but with inflorescences of uniform structure. While in the *Liliiflorae* the flowers are either solitary or loosely aggregated in small numbers, so that each flower retains its individual prominence, in the *Spadiciflorae* they are only subordinate members of a compact, highly organised inflorescence which, when the spathe is corollaceous, is commonly mistaken for a single flower (*e.g. Calla, Richardia aethiopica*). In accordance with the inconspicuous part played by the individual flowers, they are frequently reduced, particularly as regards the perianth, whose function is assumed by the axis and sheathing bracts.

FIG. 440.—*a*, Inflorescence of *Caryota urens*, greatly reduced; *b*, branch of the inflorescence of *Cocos nucifera*, with a female flower below, and male flowers above. (After DRUDE in *Nat. Pflanzenfamilien*, ¼ nat. size.)

Many species are pollinated by the wind, and these possess inconspicuously coloured, though often enormous inflorescences. In most species, however, the inflorescences are adapted to insect-pollination. The spathes and free parts of the axes, but not the individual flowers, are in such cases equipped with enticing colours, and serve as organs of attraction.

Family **Palmae** (25).—Flowers usually unisexual, of the regular Monocotyledonous type or with reduced gynœcium; aggregated in PROFUSELY BRANCHED INFLORESCENCES, which are provided with SEVERAL SPATHES. WOODY PLANTS with unbranched stems and pinnate or palmately DIVIDED leaves (Figs. 440-442).

The vegetative organs afford the most characteristic means of distinguishing the members of the family. The simple (branched only in species of *Hyphaene*) cylindrical stems bear a rosette of large pinnate or palmately divided leaves at the summit, which gives them a distinctive appearance (Fig. 442), easily recognisable and characteristic of only a few other plants (Tree-Ferns, and *Cycadaceae*). A few species are liane-like in form and mode of growth (*e.g. Calamus*). The leaves are not, like true compound leaves, divided in their early stages; they are, on the contrary, first developed as entire plicate leaves,

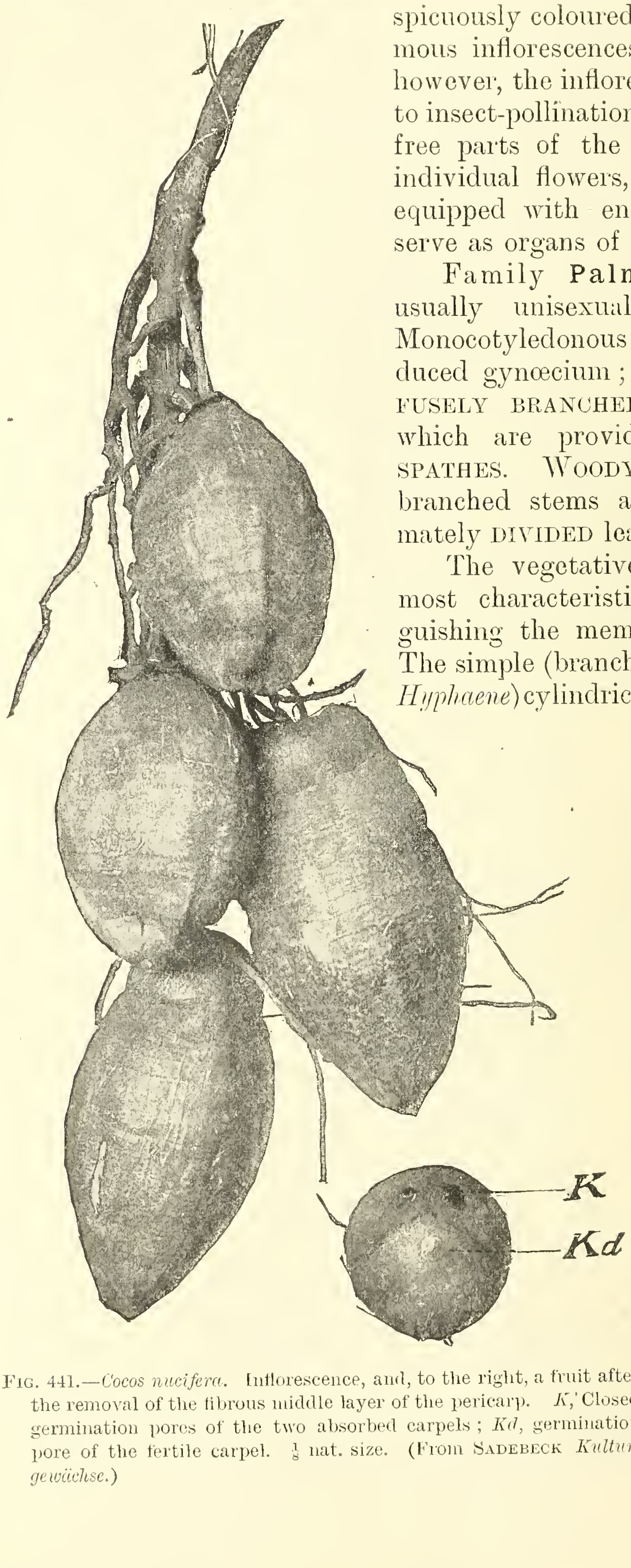


FIG. 441.—*Cocos nucifera*. Inflorescence, and, to the right, a fruit after the removal of the fibrous middle layer of the pericarp. *K*, Closed germination pores of the two absorbed carpels; *Kd*, germination pore of the fertile carpel. ⅛ nat. size. (From SADEBECK *Kulturgewächse*.)

which ultimately become slit into segments by the subsequent death and rupture of the tissue at the edges of the folds. The inflorescences (Fig. 440) are generally axillary and hang down below the leaves; in the cases where they are terminal the tree dies after the seeds ripen. In their early stages the inflorescences are entirely enveloped by the spathes, but the flowering spikes eventually protrude and bear numerous small flowers of an inconspicuous, usually yellowish, colour. Pollination is effected by the wind or by insects. The fruit is apocarpous or syncarpous; sometimes a berry, as in the case of the date; sometimes an indehiscent fruit or, like the coco-nut, a drupe (Fig. 441). From one to three seeds are produced in an ovary. The endosperm is often hard and bony in consequence of its strongly-thickened cell walls.

FIG. 442.—Group of Date Palms, *Phoenix dactylifera*, in Algiers. (From a photograph.)

GEOGRAPHICAL DISTRIBUTION.—The Palms grow chiefly in the Tropics. Only a few species thrive in the warmer countries of the temperate zones, *e.g.* the Dwarf Palm, *Chamaerops humilis*, of South Europe, and the Date Palm, *Phoenix dactylifera* (Fig. 442), cultivated to a large extent in the oases of the Sahara. On the other hand, Palms in a wild or uncultivated state, and displaying a great variety of form and size, constitute the most characteristic feature of nearly all tropical countries. There the Coco-nut Palm, *Cocos nucifera*, the most important economic plant of the Palm family, is found growing everywhere in the neighbourhood of the coast, either solitary or gregariously, in forests. The coco-nut (Fig. 441) is a gigantic drupe with a spongy, fibrous exocarp and a hard endocarp; the single seed consists of a thin seed-coat and a large, hollow fatty endosperm, in which the small embryo is embedded. Pieces of the endosperm form the Copra of commerce, while the fibre derived from the exocarp is of technical importance. Other Palms are cultivated for the sugar or wine they yield, or as ornamental trees. In the open Savannas, Palms growing singly or in small woods are of frequent occurrence. In the primeval forests, the species with tall stems grow apart from each other, in the midst of an undergrowth of smaller forms, while thorny Palm-lianes twining from tree to tree form an impenetrable jungle. Very few Palms are of special value commercially. In addition to the Coco and Date Palms may be mentioned *Elaeis guineensis*, the African Oil Palm, the oily mesocarp of whose fruit yields palm-oil; *Phytelephas macrocarpa*, of which the hard endosperm is known as vegetable ivory (Fig. 404); and *Calamus*, the stems of which are used as cane or rattan.

FIG. 443.
Spadix of *Arum maculatum*.
(After WOSSIDLO.)

OFFICINAL.—*Areca Catechu* (East Indies), with a slender stem, and pinnate, emerald-green leaves, yields SEMEN ARECAE.

FIG. 444.—*Arum maculatum* (1/3 nat. size).
POISONOUS.

Family **Araceae** (26).—Flowers often GREATLY REDUCED; inflorescence a simple spadix with a SINGLE usually corollaceous spathe. Herbs, rarely woody plants, with simple or compound leaves (Figs. 443-445).

The leaves of the *Araceae* are usually divided into stalk and lamina; they are frequently hastate in shape and generally reticulately veined. The inflorescence, which is characteristic of the family, consists of a fleshy spadix, the axis of which frequently terminates in a naked coloured prolongation (Fig. 444). The enveloping spathe is also often showily coloured; sometimes snow-white (*e.g. Richardia aethiopica*), but more frequently purple or brown, and in that case the inflorescence often emits a carrion-like stench attractive to the insects by whose aid pollination is effected. The fruit, with few exceptions, is a berry.

GEOGRAPHICAL DISTRIBUTION.—The *Araceae* are found almost exclusively in the Tropics, where they include numerous, often extremely grotesque, forms, which have, not unfrequently, a gigantic size and constitute a very large part of the herbaceous Flora of the primitive forests. Many species are terrestrial, growing gregariously in the deep shade of the woods, while others climb by means of aerial roots to the tops of the trees, or, as epiphytes, form large nest-like growths on their branches. The most remarkable of all the *Araceae* is *Amorphophallus titanum*, an herb found in Western Sumatra; it attains a height greater than that of a man, developing enormous tubers, and a purple spadix nearly $1\frac{1}{2}$ m. high. Several species of *Araceae* are cultivated as ornamental plants, *e.g. Richardia aethiopica*, the so-called Calla Lily, and the root-climber *Monstera deliciosa*.

POISONOUS.—Most of the *Araceae* are poisonous. *Arum maculatum* (Fig. 444), a tuberous herb growing in woods, has a few hastate leaves, frequently with brown spots, a greenish spathe and a fleshy spadix terminating in a naked, purple club-shaped prolongation. The flowers are monœcious; the female, at the base of the spadix; the male, forming a smaller, separate group above; while still higher up on the spadix are a few sterile flowers. In *Calla palustris*, Water Arum, a rare plant growing in bogs and swampy places, the spathe is white on the upper surface and envelops a spadix completely beset with hermaphrodite flowers.

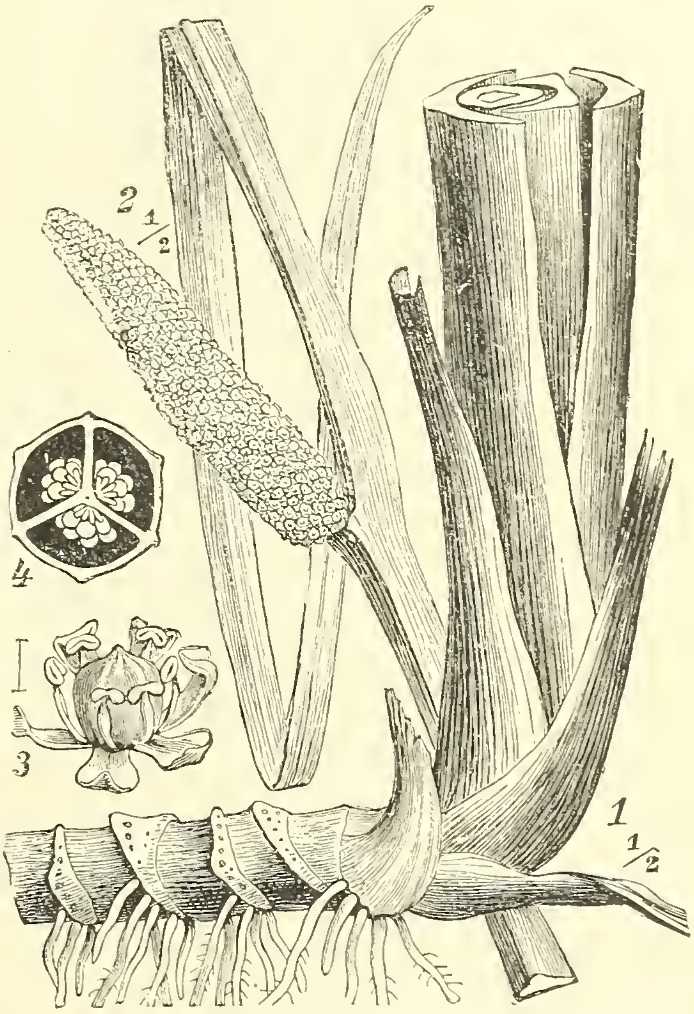


FIG. 445.—*Acorus Calamus*. 1, Rhizome; 2, inflorescence; 3, flower; 4, ovary in transverse section.—*OFFICINAL*. (After WOSSIDLO.)

OFFICINAL.—From *Acorus Calamus*, Sweet Flag (Fig. 445), a marsh plant with creeping rhizome, narrow leaves, and greenish inflorescences of hermaphrodite flowers, RHIZOMA CALAMI and OLEUM CALAMI are obtained.

Family **Lemnaceae** (^{27}).—Duckweeds. Floating plants occurring on still water;

they have a disc-shaped vegetative body, and are in some cases devoid of roots. Monœcious, naked flowers enclosed by a spathe. *Lemna, Wolffia.*

Order 3. Glumiflorae

Flowers hypogynous, hermaphrodite or unisexual, NAKED OR WITH REDUCED PERIGONE; ovary unilocular, containing ONE OVULE; inflorescence with MANY SMALL flowers, and NUMEROUS GLUMACEOUS BRACTS. For the most part herbs with LINEAR PARALLEL-NERVED leaves.

Nearly all the *Glumiflorae* have a grass-like appearance, *i.e.* they are herbaceous, rarely woody plants, with narrow pointed leaves, and have inconspicuous inflorescences bearing small flowers and numerous scale-like bracts. The bracts are dry, green or brownish, in part sterile and to some extent serving as subtending leaves to the lateral axes and flowers. They usually constitute the most noticeable part of the inflorescence, particularly when, as in many true Grasses, they are prolonged into an awn (arista). The inconspicuous colour of the inflorescence, the gentle swaying movements of the anthers pendent from the long filaments hanging down between the bracts, the abundant dry pollen, and the well-developed papillæ on the large stigmas are all directly correlated with the wind-pollination common to all *Glumiflorae* (Fig. 450).

As in most thick small-flowered inflorescences, the individual flowers of the *Glumiflorae* are simply constructed, evidently in this case in consequence of reduction. In none of the flowers of this order is the regular Monocotyledonous type presented in an unmodified form; in all, at least one or the other of the whorls is entirely suppressed. The perigone, no longer exercising its protective office, now assumed by the bracts, consists only of bristles or small scales, or is altogether absent. The andrœcium has sometimes all the six stamens, but usually, by the suppression of the inner whorl, it is reduced to three; the gynœcium may also possess the full number of three carpels, although frequently only two, and usually only one, are present. In most cases a dry, indehiscent fruit (caryopsis) is produced, with one seed containing a mealy albumen.

A similar grass-like habit is shown by other Monocotyledons, especially by the *Juncaceae, Typhaceae, Sparganiaceae,* which were on that account formerly regarded as the nearest allies to the Grasses; the structure of their flowers, however, has assigned them to another position in the system of classification. Of the two families now forming this order, the *Cyperaceae* have suffered less reduction in the structure of their flowers than the *Gramineae*. The latter do not appear to have been derived from the *Cyperaceae* by a continued process of reduction.

Family **Cyperaceae.**—Flowers usually DICLINOUS, naked or with reduced perigone; ovary DI- or TRIMEROUS with ANATROPOUS ovules. Pericarp NOT ADHERENT to the seed; embryo WITHOUT SCUTELLUM, and ENCLOSED IN ENDOSPERM. Herbs with triangular axes, which are NOT HOLLOW, and rarely swollen at the nodes; leaves often three-ranked, with CLOSED leaf-sheaths, and either with or without a reduced ligule. Inflorescences of varying character, usually WITHOUT BRACTEOLES (Fig. 446, 447).

FIG. 446.—*Carex arenaria.* 1, Flowering plant; 2, male flower with bract (glume); 3, female flower; 4, pistil; 5, bract of female flower; 6, 7, male and female flower of *Carex hirta.* (After WOSSIDLO.)

The *Cyperaceae* are, for the most part, perennial herbs with profusely branched rhizomes and stiff or hard, sharp-edged leaves. The rhizome gives rise to tufts of sterile leaves, together with fertile shoots, which, according as the branches of the rhizome are long or short, cover extended areas or form isolated groups. At the base of the fertile shoots the internodes are short, while the whole upper portion of the shoot consists of but one internode, which is greatly elongated and bears the inflorescence. The inflorescences are variously constructed, sometimes a simple spike, sometimes compound, consisting of spikelets united into spikes, heads or panicles. Subtending bracts (glumes) are present in all inflorescences; sterile bracteoles only in a few genera. The flowers are in most cases monœcious, both sexes being united in the same spike or occurring on different spikes.

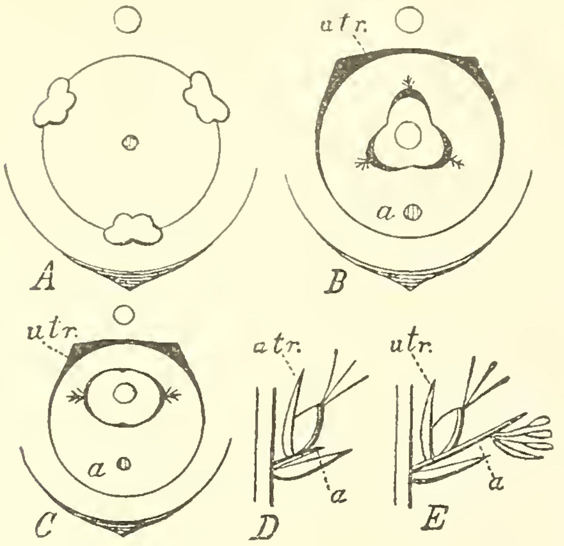


Fig. 447. *A*, Floral diagram of a male flower of *Carex*; *B*, of a female flower with three stigmas; *C*, of a female flower with two stigmas; *D*, diagram of a female flower of *Carex*; *E*, diagram of the hermaphrodite spikelet of *Elyna*; *a*, secondary axis; *utr*, utriculus or bract of the secondary axis.

Representative Sub-Families and Genera.—(1) *Scirpoideae*. Flowers hermaphrodite, often with perigone. *Scirpus*, *Cyperus*, *Eriophorum*, with a perigone consisting of bristles which, after the maturity of the flower, grow out into long hairs. (2) *Caricoideae*. Flowers unisexual, always naked; *Carex*.

Geographical Distribution.—The *Cyperaceae* or Sedge Family are represented throughout the world, growing frequently in damp meadows, in marshes, and along the margins of streams. They are worthless as fodder plants on account of their hard leaves. The genus *Carex* is the most common and comprises the greatest number of species. The family contains no plants of economic value. The papyrus used by the ancient Egyptians was made of thin strips of the firm pith of *Cyperus Papyrus*.

Family **Gramineae** (28).—Flowers usually HERMAPHRODITE, naked; ovary monomerous, with a slightly CAMPYLOTROPOUS ovule; pericarp ADHERENT to the seed; embryo with SCUTELLUM, LATERALLY IN CONTACT WITH THE ENDOSPERM. Herbs, rarely shrubs or trees; axes with HOLLOW internodes. Leaves two-ranked, having usually a ligule and an OPEN sheath with a node-like thickening at the base. Inflorescences compound, consisting of spikelets aggregated in spikes or panicles; BRACTEOLES PRESENT (Figs. 448-455).

The *Gramineae* or true Grasses are for the most part perennial herbs, with a profusely branched rhizome creeping horizontally in the soil, and giving rise to sterile shoots in the form of tufts of leaves, and also to fertile shoots, which are usually unbranched but provided with leaves, and divided throughout their whole length into internodes.

The annual species of *Gramineae* are not so numerous; they do not have rhizomes nor form the sterile tufts; shrub- or tree-like forms are still less frequent. A membranous ligule is always developed at the junction of the lamina with the leaf-sheath.

The inflorescences of the *Gramineae* in their entirety are spike-, raceme-, or panicle-like in character, and are always composed of an aggregation of secondary inflorescences or SPIKELETS (Fig. 449). Each spikelet usually bears several flowers, and also a number of bracts

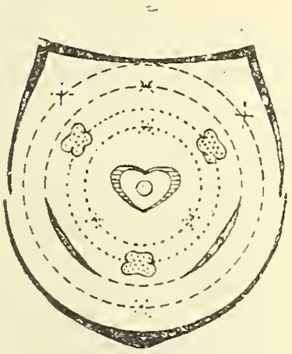


FIG. 448.—Floral diagram of the *Gramineae* (*Avena*), in accordance with the hypothesis that the lodicules represent perigone leaves. The absent members are represented by ×.

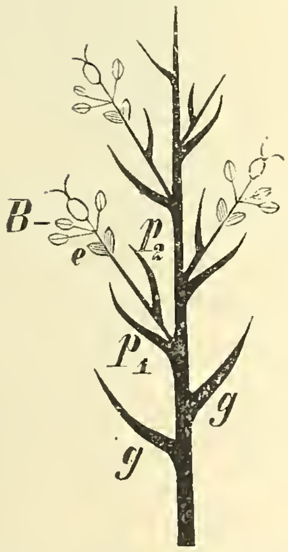


FIG. 449.—Diagrammatic representation of a Grass spikelet. g, The glumes; p_1 and p_2, the inferior and superior paleae; e, lodicules: B, flower.

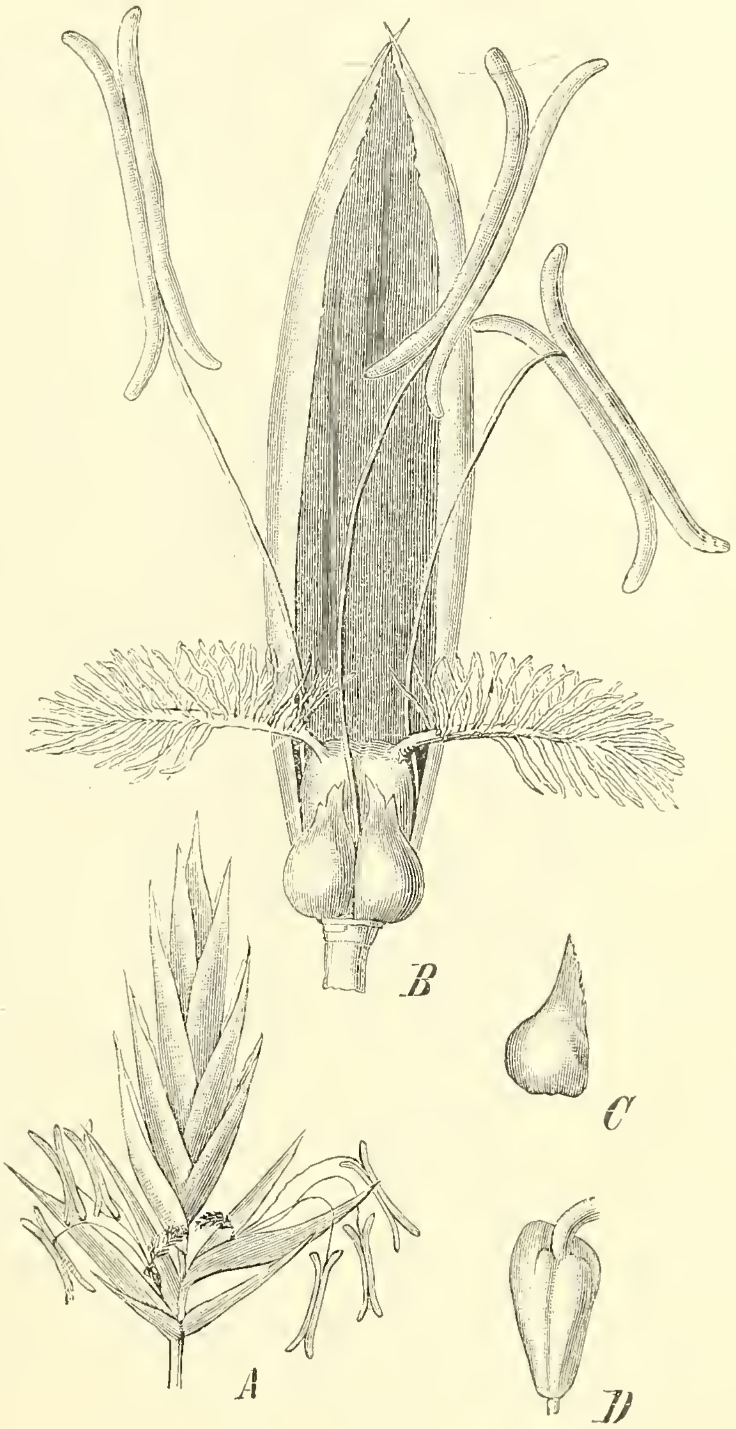


FIG. 450.—*Festuca pratensis*. *A*. Spikelet (compare Fig. 449) with two open flowers, below which the two sterile glumes are seen (× 3); *B*, Flower; the two lodicules are in front, the superior palea behind; the ovary bears two feathery stigmas (× 12); *C*, a single lodicule (× 12); *D*, ovary seen from the side with the stalk of one of the removed stigmas (× 12).

arranged in two rows. The two lower bracts, less frequently the three lower of each spikelet, are sterile, and are known as GLUMES. These are followed by a varying number of fertile bracts subtending flowers, and termed INFERIOR PALEÆ, sometimes also called flowering glumes. The inferior or outer paleæ are often prolonged into awns. Immediately below the flower the short flower-stalk bears a bracteole or SUPERIOR PALEA, which is always devoid of an awn (Fig. 450, *B*), and two scales, the LODICULES (*C*). The lodicules are regarded as a reduced perigone. At the time of flowering the lodicules become swollen, and by forcing apart the paleæ and glumes they bring about the opening of the flowers. All the axial portions of the spikelets are short, so that the bracts, packed one immediately over the other, are only partially visible.

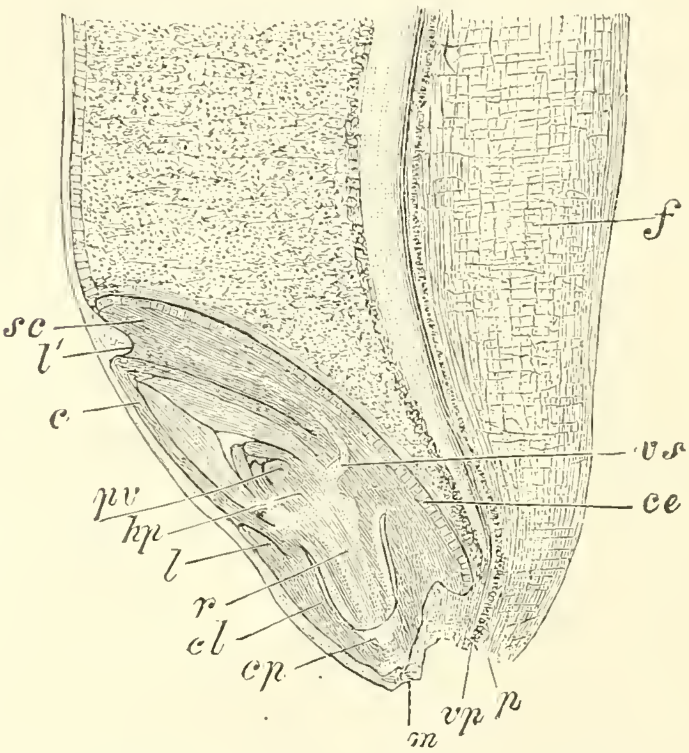


FIG. 451.—Part of median longitudinal section of a grain of wheat, showing embryo and scutellum (*sc*); *vs*, vascular bundle of scutellum; *ce*, its cylinder epithelium; *l'*, its ligule; *c*, sheathing part of the cotyledon; *pv*, vegetative cone of stem; *hp*, hypocotyl; *l*, ligule; *r*, radicle; *cl*, root-sheath; *m*, micropyle; *p*, funiculus; *vp*, its vascular bundle; *f*, lateral wall of groove. (× 14.)

The androecium consists usually of three stamens, each with a large elongated anther attached below the middle to the apex of the slender filament. The ovary has two, rarely three, branching stigmas situated either directly upon the ovary itself, or borne on a short style (Fig. 450, *B*). The pericarp is leathery, and assumes the functions usually performed by the seed-coat, which is thin and adherent to it. In many cases (*e.g.* in most species of Barley) the pericarp and paleæ also adhere. On germination a shield-like appendage of the cotyledon, the scutellum, remains within the seed and absorbs the endosperm (Fig. 451).

Streptochaeta, a Brazilian genus which has probably retained a likeness to the ancestral forms of this order, possesses, according to CELAKOVSKY and GOEBEL, a complete Monocotyledonous flower; the perigonial leaf falling immediately above the bract is, however, only recognisable as a rudiment in the young flower. A trimerous perianth corresponding to the inner whorl of the Monocotyledonous flower occurs in several genera of Grasses. Possibly the so-called superior pale is derived from the cohesion of two perianth segments of the outer whorl.

GEOGRAPHICAL DISTRIBUTION.—Like the *Cyperaceae*, the *Gramineae* are widely distributed over the whole world. They appear in the most varied situations, in particular in meadows and fields, of which they form the principal vegetation.

Among the most important meadow-grasses the following may be mentioned: *Poa pratensis*, Common Meadow Grass or Kentucky Blue Grass; *Agrostis vulgaris*, Red-top; *Alopecurus pratensis*, Meadow Foxtail; *Phleum pratense*, Timothy; *Dactylis glomerata*, Orchard Grass; *Briza media*, Quaking Grass; *Anthoxanthum odoratum*, Sweet Vernal; *Lolium perenne*, Rye Grass; *Holcus lanatus*, Velvet Grass; *Arrhenatherum elatius*, False Oat Grass; *Avena pubescens* and *A. flavescens*, the Yellow Oat Grass, etc. The arborescent grasses of the genus *Bambusa* and its allies form extensive grooves in the Tropics, or the smaller forms grow in the shade of the primitive

FIG. 452.—Cereals. *A*, Rye, *Secale cereale*; *B*, Spelt, *Triticum Spelta*; *C*, Two-ranked Barley, *Hordeum vulgare, distichum*; *D*, Wheat, *Triticum vulgare*.

forests. The most important of the cereal grasses (Fig. 452) grow in the Temperate Zone: Wheat, *Triticum vulgare*, with numerous varieties and races, *e.g. T. turgidum, T. durum, T. polonicum;* Spelt or German Wheat, *T. Spelta;* Amel corn or French rice, *T. dicoccum;* One-grained Wheat, *T. monococcum;* Rye, *Secale cereale;* Barley, *Hordeum vulgare*, in several varieties and races, as *H. hexastichum, H. distichum*, etc.; Oats, *Avena sativa;* Maize, *Zea Mais;* and numerous fodder-plants. The native condition of the cereals is unknown, except in the case of *Hordeum distichum*, the two-rowed Barley, which is found in Asia, and Maize, which is of American origin. The other cereals were probably indigenous to Asia or Eastern Europe. Rice, *Oryza sativa* (Fig. 453), originally derived from the East Indies, and *Saccharum officinarum*, Sugar-cane (Fig. 454), are cultivated in the Tropics and sub-tropical zones. The latter is a perennial plant with solid internodes filled with parenchyma, from the cell-sap of which part of the cane-sugar of commerce is obtained by a process of evaporation and subsequent refining (cf. *Beta vulgaris*). The Indian Millet, *Andropogon Sorghum*, and the different species of *Bambusa*, whose stems furnish a convenient building material, while their hollow internodes serve for household utensils, are also chiefly tropical.

FIG. 453.—*Oryza sativa.* 1, inflorescence; 2, spikelet. (After WOSSIDLO.)

FIG. 454.—*Saccharum officinarum* (greatly reduced). 2, Flower after removal of the paleæ.—*OFFICINAL.* (After WOSSIDLO.)

POISONOUS.—*Lolium temulentum*, Bearded Darnel (Fig. 455), an annual grass with narrow, elongated inflorescences of a green colour. The seeds are poisonous, as are also those of *L. linicola*, a weed only found growing in Flax fields. Both may be distinguished from the other harmless species of *Lolium, e.g. L. perenne*, Rye Grass, by the absence of tufts of sterile leaves.

OFFICINAL. —*Saccharum officinarum* (Fig. 454) yields SACCHARUM; the germinating grain of *Hordeum vulgare*, MALTUM; *Agropyrum repens*, Couch Grass, RHIZOMA or RADIX GRAMINIS. The starch derived from the seed of *Triticum vulgare* is the officinal AMYLUM TRITICI; *Oryza sativa*, AMYLUM ORYZAE.

FIG. 455.—*Lolium temulentum.*—*POISONOUS.*

Order 4. Helobiae

Flowers hypogynous, less frequently epigynous, actinomorphic, with perianth; STAMENS USUALLY MORE THAN SIX; CARPELS USUALLY MORE THAN THREE, in hypogynous flowers FREE; seeds WITHOUT ENDOSPERM; embryo with LARGE HYPOCOTYL.

The *Helobiae* are marsh- or water-plants, sometimes of a grass-like appearance, sometimes with broad leaves. According to the mode of pollination, whether effected by the wind, water, or insects, the perianth is either small and of a greenish colour, or large and differentiated into a calyx and corolla. The structure of the flowers may be regarded as a modification of the Monocotyledonous type, resulting phylogenetically from the splitting of the stamens and carpels. Flowers exhibiting reduction also occur in this order.

Family **Alismaceae.**—Flowers HYPOGYNOUS, HERMAPHRODITE, with perianth differentiated into CALYX and COROLLA; stamens 9 (6 + 3) or more; carpels free, numerous, sometimes arranged in spirals. Fruit dry and indehiscent, rarely a capsule (Figs. 456, 457).

Members of this family are found in all zones growing in marshes or shallow water. As representative species may be mentioned *Alisma Plantago*, Water

Plantain, *Sagittaria sagittifolia,* Arrow-head, and *Butomus umbellatus,* Flowering Rush.

Family **Juncaginaceae.**—Habit grass-like, perigone calycoid. *Triglochin.*

Family **Hydrocharitaceae.**—Flowers EPIGYNOUS, usually UNISEXUAL; perianth consisting of both CALYX and COROLLA, or the latter may be suppressed; stamens three to many; ovary of three or more carpels. Fruit with irregular dehiscence, commonly many-seeded.

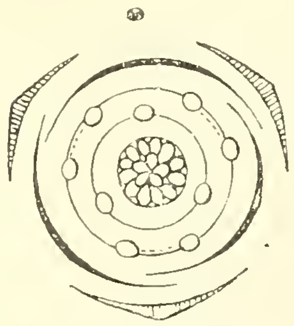


Fig. 456.—Floral diagram of *Echinodorus parvulus,* one of the *Alismaceae.* (After Eichler.)

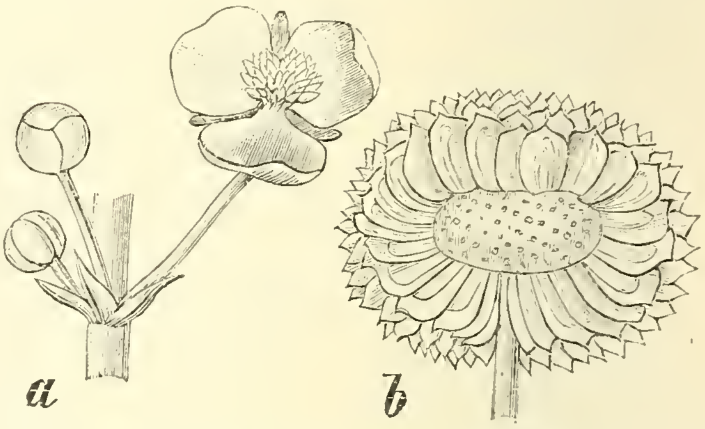


Fig. 457.—*Sagittaria sagittifolia.* *a*, Flower; *b*, fruit after removal of part of the carpels. (Magnified.)

Aquatic Plants.—*Hydrocharis morsus-ranae, Stratiotes aloides. Elodea canadensis* has been introduced into Europe from America.

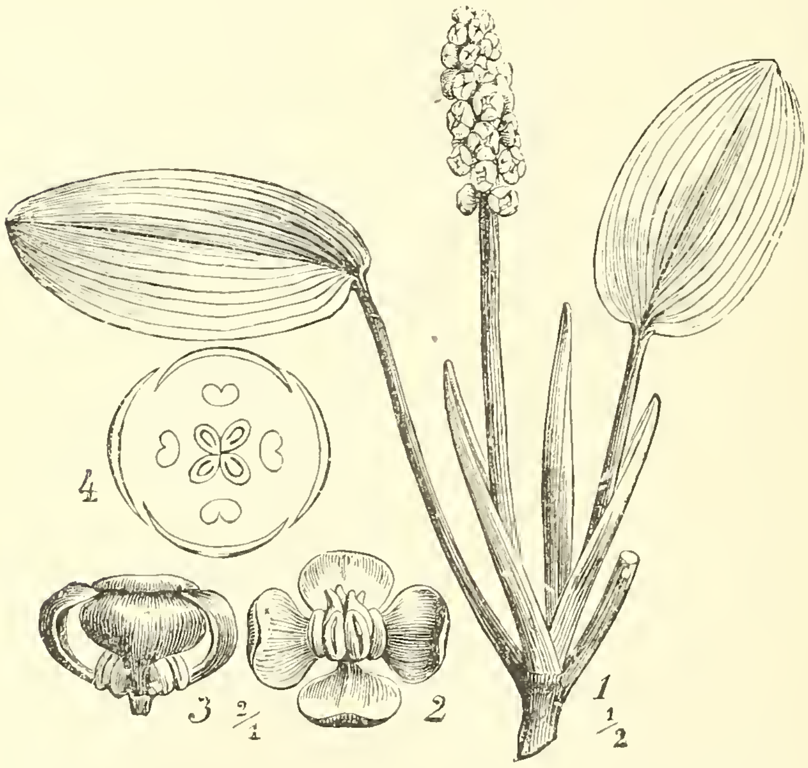


Fig. 458.—*Potamogeton natans.* 1, Apex of flowering shoot; 2, flower viewed from above; 3, flower viewed from the side; 4, diagram of flower. (After Wossidlo.)

Family **Potamogetonaceae.**—Flowers HYPOGYNOUS, unisexual, or hermaphrodite, usually NAKED or with REDUCED, CALYCOID PERIGONE; andrœcium and the apocarpous gynœcium ONE- TO FOUR-MEROUS. Ripe carpels drupaceous, one-seeded (Fig. 458).

The members of this family constitute a chief part of the fresh-water flora of all zones. *Potamogeton,* Pond-weed, and *Zannichellia,* Horned Pond-weed, are familiar fresh-water genera. Some species are found in salt water, where they cover extended areas in the neighbourhood of the coast with a submerged vegetation, *e.g.* *Zostera marina,* Grass-Wrack or Eel-grass, found in salt water throughout all zones. It is used for stuffing cushions, etc., and is the only plant of economic value in the whole order.

The small family **Najadaceae** (flowers diclinous, one stamen, one ovary) is closely related to the preceding, which it resembles in appearance and habit. *Najas major* may serve as an example.

Order 5. Scitamineae

Flowers EPIGYNOUS, ZYGOMORPHIC or ASYMMETRICAL; andrœcium REDUCED, often PARTLY PETALOID; ovary usually TRILOCULAR; seeds with perisperm.

The *Scitamineae* are herbs, usually with perennial rhizomes and with large pinnately-veined leaves. The flowers are adapted to insect-pollination; the perianth is in some cases differentiated into a calyx and corolla, or developed as a corollaceous perigone. The structure of the andrœcium is especially characteristic. Although in certain cases (*e.g.* in the flowers of the Banana) it differs from the regular type merely in the absence or staminodial development of the posterior stamen, in the majority of the *Scitamineae* only one fertile stamen is present. The other members of the andrœcium are then either suppressed or they assume the form of PETALOID STAMINODIA, which give the flowers a distinctive shape and appearance (Figs. 459, 461, *C*). In the *Cannaceae* and *Marantaceae* even the fertile stamen is petaloid and bears only a half-anther. The fruit is variously developed.

FIG. 459.—Flower of *Canna iridiflora*. *f*, Ovary; *k*, calyx; *c*, corolla; *l*, labellum; $st_{1\text{-}3}$, the other staminodia; *a*, fertile stamen; *g*, style. (½ nat. size.)

Family **Musaceae.**—Flowers ZYGOMORPHIC, with FIVE FERTILE stamens. Tropical herbs, arborescent in appearance, rarely true trees, with enormously large leaves. The Banana (*Musa sapientum* and *Musa paradisiaca*) is largely cultivated in all tropical countries for the sake of its edible baccate fruit.

Family **Cannaceae.**—Large-leaved herbs with asymmetrical flowers, often cultivated (Fig. 459).

Family **Marantaceae.**—Leaves with peculiar swellings at the articulations, often variegated. AMYLUM MARANTAE, West Indian Arrowroot, is obtained from *Maranta Arundinacea*.

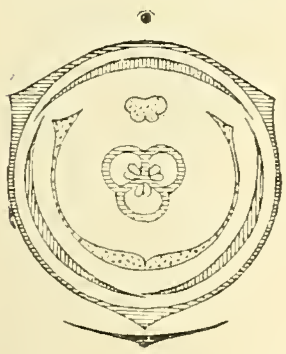


FIG. 460.—*Zingiberaceae*. Floral diagram (*Zingiber*).

Family **Zingiberaceae.**—Flowers ZYGOMORPHIC; THE POSTERIOR STAMEN OF THE INNER WHORL ALONE FERTILE, AND THE TWO

LATERAL, INNER STAMENS CONNATE AND TRANSFORMED INTO A TONGUE-SHAPED LEAF, THE LABELLUM; the outer whorl of stamens staminodial or absent (Figs. 460, 461).

The members of this family are aromatic herbs, with rhizomes.

FIG. 461.—*Zingiber officinale.* *A*, Entire plant (½ nat. size); *B*, flower; *C*, labellum; *D*, transverse section of ovary.—*OFFICINAL.* (After BERG and SCHMIDT.)

The flowers are aggregated in inflorescences of various types, and are usually large and highly coloured. The splendour of their appearance is due to the prominent position taken by the labellum (Fig. 461, *B*, *C*), which is considerably larger than the leaves of the perianth. The fruit is a three-valved capsule, rarely a berry. The seeds are provided with an aril (Fig. 405).

GEOGRAPHICAL DISTRIBUTION.—The members of the *Zingiberaceae* are all tropical. They are represented by numerous species and individuals in the forests of South Asia, which they beautify by their magnificent flowers and foliage. Many species are cultivated in hot-houses as decorative plants, others are valuable for their aromatic properties, *e.g.* ginger, cardamom.

OFFICINAL.—*Zingiber officinale* (East Indies, Fig. 461) supplies RHIZOMA ZINGIBERIS; *Curcuma Zedoaria* (East Indies), RHIZ. ZEDOARIAE: *Alpinia officinarum* (from the island of Hainan, China), RHIZ. GALANGAE: *Elettaria Cardamomum* (East Indies). FRUCTUS CARDAMOMI.

Order 6. Gynandrae

Flowers EPIGYNOUS, hermaphrodite, ZYGOMORPHIC; perigone corollaceous; andrœcium REDUCED TO THE THREE ANTERIOR MEMBERS, consisting usually of one fertile stamen and two staminodia, ADHERENT TO THE STYLE AND FORMING A COLUMN; ovary usually UNILOCULAR, with parietal placentation; fruit, a capsule; seeds EXCEEDINGLY NUMEROUS AND SMALL, without albumen; embryo UNSEGMENTED.

Family **Orchidaceae** (29).—Characteristics the same as for the order (Figs. 462-467).

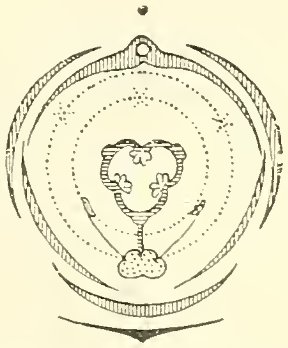


FIG. 462.—*Orchidaceae.* Floral diagram (*Orchis*).

The Orchids are all herbs; they vary greatly in external appearance and have racemose, usually spike-like inflorescences. The flowers are almost always pollinated by insects, and to this end have developed the most complicated contrivances. The corollaceous perigone exhibits endless variation. The posterior leaf of the inner whorl is often especially characterised by its size, form, and colour; like the similar but not homologous staminodial organ of the *Zingiberaceae*, it is termed a LABELLUM; it is frequently drawn out below into a sac-shaped cavity or spur (Fig. 463, a, *f*). In its rudimentary condition the labellum is uppermost, but, as a rule, it acquires ultimately an anterior position in consequence of the torsion of 180° suffered by the inferior ovary, or as a result of the tilting over of the whole flower. In the andrœcium only the anterior stamen of the outer whorl and the two lateral members of the inner whorl are developed; these two lateral members are usually transformed into sterile, lobed, or tooth-like prominences (b, *p*), while the central stamen alone is fertile and bears an anther (*e.g. Orchis*); less frequently, the central of the three staminal members of the andrœcium is sterile, while the two lateral are fertile (*Cypripedium*, Lady's Slipper). The GYNOSTEMIUM (b) formed by the union of the stamens with the tips of the carpels is sometimes developed as a column; sometimes, as in *Orchis*, it is short and barely elevated above the receptacle. It bears at its apex the stigma and the anther, or a pair of anthers as the case may be. The pollen is rarely powdery, consisting of separate grains (*e.g. Cypripedium.*) All the pollen-grains of each theca are usually united by a viscid substance into a club-shaped mass or POLLINIUM (**c**), attached above or below to a mucilaginous filament termed the CAUDICLE (**c**, *r*). In a few cases several pollinia are present. The three-lobed stigma (**b**, *h*) is situated directly below the anther. The two lateral lobes are always normally developed and destined to receive the pollen, while the anterior lobe has frequently the form of a pouch-shaped beak or ROSTELLUM (**b**, *l*), in which one or two small masses of sticky mucilage (*q*), the GLANDULÆ (*retinacula*), are formed by the disorganisation of the tissue. To these sticky glandulæ are attached the caudicles with their pollinia. The whole structural development of the flower represents an adaptation to insect-pollination. When an insect inserts its proboscis in the nectaries of the labellum, the glandulæ with their stalked pollinia become glued to it, and the pollen is thus applied to the next flower visited by the insect. Similarly, by inserting a pointed instrument in the spur, a lead-pencil for example, the pollinia will be found attached to it on its withdrawal. The capsule is often leathery, and in dehiscing splits into six valves. The embryo is usually spherical and exhibits no differentiation into hypocotyl and cotyledon.

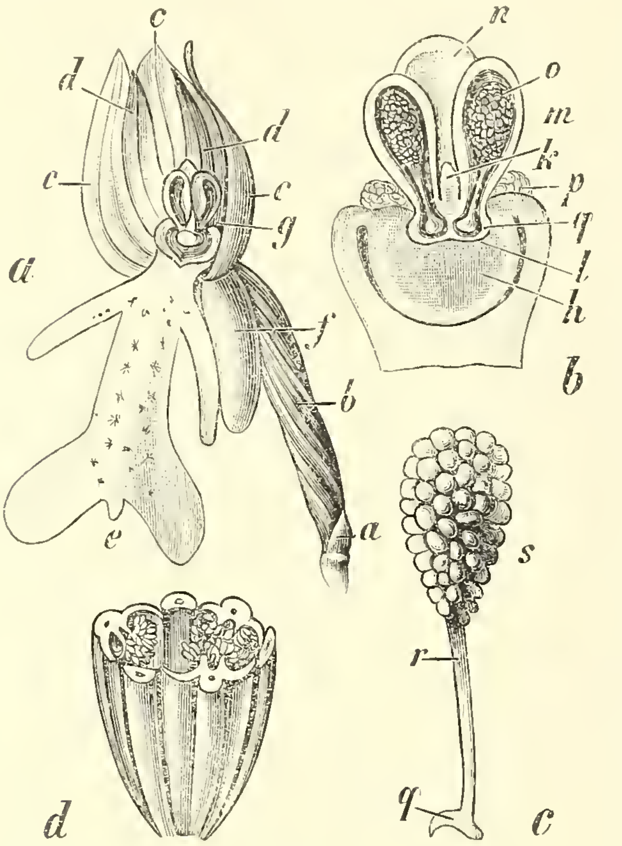


Fig. 463.—*Orchis militaris*. **a**, Flower: *a*, bract; *b*, ovary; *c*, the outer, and *d*, the two anterior inner perigone leaves; *e*, labellum with the spur *f*; *g*, gynostemium. **b**, Flower after removal of all of the perigone leaves with exception of the upper part of the labellum; *h*, stigma; *l*, rostellum; *k*, tooth-like prolongation of the rostellum; *m*, anther; *n*, connective; *o*, pollinium; *q*, glandula; *p*, staminodium. **c**, A pollinium: *r*, caudicle: *s*, pollen. **d**, Ovary in transverse section. (After BERG and SCHMIDT.)

Many of the indigenous species have underground tubers (*e.g. Orchis*). As a rule, two tubers are present, formed by the union of several roots; according as the coalescence is more or less complete, they are ovate and smooth (Fig. 465), or palmately divided (Fig. 464). One of the tubers, the older mother-tuber, is dark-coloured and flaccid; it bears the floral shoot and afterward dies. The other, the daughter-tuber, is firmer, lighter-coloured, and provided with an apical bud. It remains dormant in the soil over winter, and in the succeeding spring gives rise to an aerial shoot, and then, after producing a new daughter-tuber, acquires in turn the structure and appearance of a mother-tuber in consequence of the exhaustion of the accumulated reserve material of its cells.

SUB-FAMILIES AND REPRESENTATIVE GENERA.—(1) *Diandrae.* Two (rarely three) fertile stamens. All three stigmatic lobes susceptible of pollination. *Cypripedilum.* (2) *Monandrae.* One fertile stamen. Of the three stigmatic lobes, one continues rudimentary or develops as a rostellum. *Orchis,* with spurred labellum; *Ophrys,* without spur, the flower resembling an insect; both genera, and similarly *Gymnadenia*, *Platanthera*, and others, with tubers: *Cephalanthera*

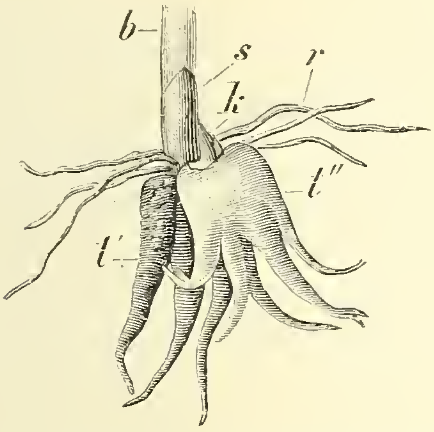


FIG. 464.—Root-system of *Orchis latifolia.* *b*, Base of stem; *s*, cataphyllary leaf; *t'*, old. *t''*, young tubers; *k*, bud; *r*, roots.

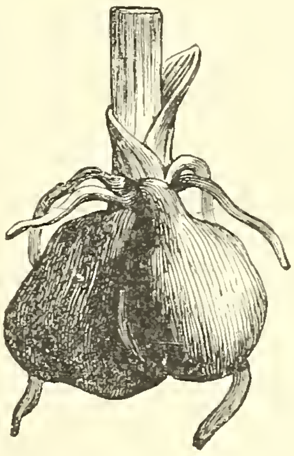


FIG. 465.—Root-system of *Orchis morio.*—*OFFICINAL.* (After WOSSIDLO, nat. size.)

FIG. 466.—*Gongora galeata,* an epiphytic orchid. (After PFITZER in *Nat. Pflanzenfamilien*, ⅕ nat. size.)

FIG. 467.—*Vanilla planifolia.* Flowering shoot (⅓ nat. size).—*OFFICINAL.* (Reduced from a figure by BERG and SCHMIDT.)

and *Epipactis*, with creeping rhizome. *Neottia*, *Epipogon*, and *Coralliorhiza* are humus plants, either poor in chlorophyll or wholly devoid of it. *Vanilla* (see under Officinal).

Geographical Distribution.—This family inhabits chiefly the Tropics, where thousands of its species are found growing as epiphytes upon trees. The roots of such epiphytes (Fig. 466) attach themselves to the bark and are enveloped by a velamen, which greedily absorbs water ; while, in many cases, the stems are tuberously swollen and serve as water-reservoirs, accumulating water in their cells and transmitting it to the leaves in dry weather. Terrestrial Orchids, on the other hand, are more numerous outside of the tropical zone, particularly in the drier regions of Southern Africa and the countries adjoining the Mediterranean, which are especially characterised by the profusion of their tuberous and bulbous plants (cf. *Liliaceae*).

Officinal.—The unripe fruit of *Vanilla planifolia* (Fig. 467) is the officinal Fructus Vanillae. The Vanilla is indigenous to Mexico, but is now cultivated in all tropical countries. It climbs by means of its aerial roots, like the Ivy. The ovate, not the divided, tubers of several species of *Orchis* and allied plants found in Europe and Asia Minor are used as Salep, Tubera Salep.

Sub-Class II

Dicotyledones (1, 2)

Flowers generally constructed after the PENTAMEROUS, pentacyclic type. Embryo with TWO COTYLEDONS. Herbs and woody plants with OPEN vascular bundles exhibiting, in cross-sections of the stems, a CIRCULAR arrangement, and also almost always with a cambium which intersects the bundles (Fig. 468). Leaves usually with RETICULATE VENATION (Fig. 469).

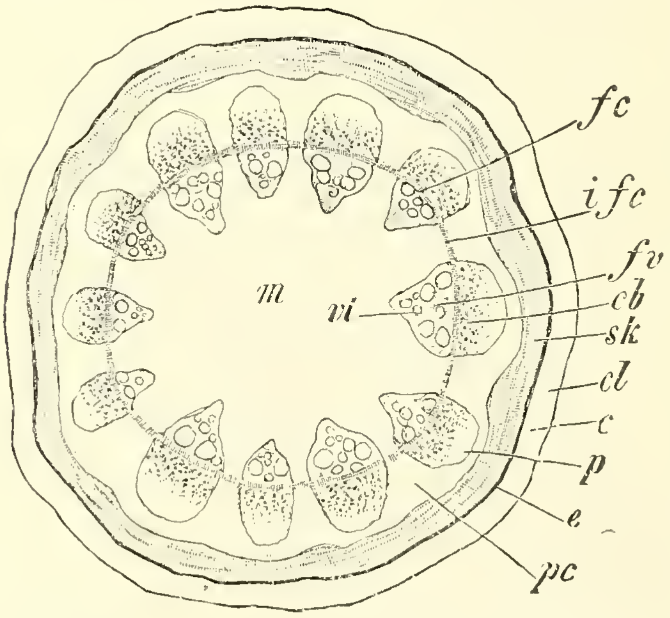


Fig. 468.—Transverse section of a young stem of *Aristolochia Sipho* (cf. p. 112).

The seeds are variously constructed, sometimes with, sometimes without albumen. The embryo may be large or small ; in some parasites and saprophytes it is unsegmented, but otherwise it is differentiated into radicle, hypocotyl, and two cotyledons. On germination, the cotyledons remain in some cases enclosed within the seed, in others they become green and unfold above the surface of the soil.

The primary root is usually retained, and may be distinguished from the lateral roots by its larger size and more vertical growth.

The stem of most Dicotyledons is more or less profusely branched.

(For an account of the arrangement (Fig. 468) of the vascular bundles and of their structure cf. pp. 112 and 105. The secondary thickening is described on p. 122.)

The leaves are alternate or whorled. They often have stipules, but rarely leaf-sheaths. The lamina is simple or compound, entire or more or less irregular in outline.

In the majority of cases the structure of the flowers may be referred to the PENTACYCLIC, pentamerous type, although flowers with whorls, consisting of two to six or more members, also occur. When more than five members are present in a whorl the modification of the normal structure is usually due to splitting; when less than five, to suppression. There are also some flowers which normally have less than five members in the floral whorls. In the most simply constructed Dicotyledonous flowers (*Amentaceae*) the number of members composing the whorls is subject to variation.

In the oldest forms a corolla is typically absent; in the more highly developed the perianth is usually differentiated into a calyx and corolla. More rarely the perianth is simple, by the suppression of one whorl, or is developed as a double calycoid or corollaceous perigone. The median sepal with few exceptions (*Papilionaceae*, *Lobeliaceae*) occupies a posterior position.

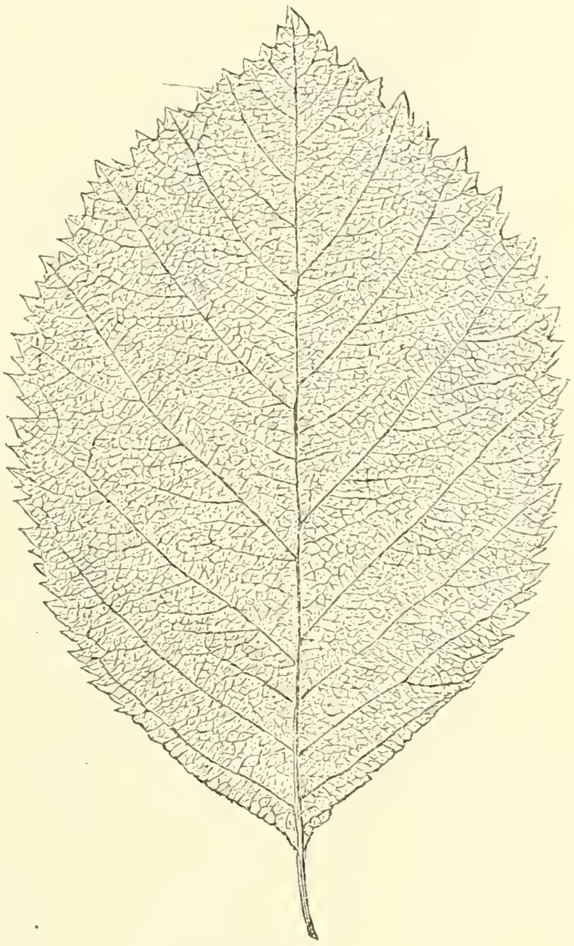


FIG. 469.—Leaf with reticulate venation. ($\frac{3}{4}$ nat. size.)

The Dicotyledons are divided into the two groups, *Choripetalae*, with the corolla segments free, and *Sympetalae*, with the segments of the corolla united.

Group 1. Choripetalae

Perianth single or double, and then usually polyphyllous.

Order 1. Amentaceae

Flowers hypogynous or epigynous, UNISEXUAL, SMALL, NAKED, or with CALYCOID PERIGONE; the male in CATKINS (amenta); the female in various inflorescences. Number of stamens variable, rarely the same as that of the perigone leaves. Gynœcium TWO- TO SIX-MEROUS. The pollen-tube usually enters the ovule by the chalaza, not by the micropyle. Seeds without endosperm.

The *Amentaceae* are all woody plants with alternate leaves. The male inflorescences are characteristic of this order; they have the form of catkins, bearing the small flowers in the axils of scale-like bracts. The female flowers are sometimes aggregated into catkins, as in the Willow; in other cases into capitate or spike-like inflorescences. The fruit is usually a one-seeded nut, rarely a capsule or drupe.

FIG. 470.—*Salix viminalis.* *A*, Flowering male-shoot (nat. size); *B*, male flower with subtending bract (magnified); *C*, female inflorescence; *D*-*E*, female flowers (magnified); *F*, fruit (nat. size); *G*, the same magnified; *H*, seed (magnified).

FIG. 471.—*Populus tremula.* 1, Male inflorescence; 2, female inflorescence; 3, male flower; 4, female flower; 5, the same in longitudinal section; 6, fruit; 7, the same after dehiscence; 8, seeds; 9, diagram of male flower. (After WOSSIDLO.)

The diclinous flowers, the absence or imperfect development of the perianth, the variable number and often irregular arrangement of the parts of the flower in the same or in allied species, the almost uniform wind-pollination, the small degree of modification exhibited by the flowers adapted to pollination by insects, and the chalazogamy make it probable that of all the Dicotyledons the *Amentaceae* differ least widely from the primitive form, and represent phylogenetically the lowest stage of development.

The essential variations exhibited within the order are limited to the female flowers, which are sometimes hypogynous, sometimes epigynous, and possess a septated or unseptated ovary, a single ovule or a number of ovules in different positions. These distinctions are utilised in classifying the different families.

Family **Salicaceae.**—Flowers HYPOGYNOUS, diœcious; perianth absent; DISC cupular or consisting of scales; ovary dimerous, UNILOCULAR WITH NUMEROUS PARIETAL OVULES; fruit a capsule; seeds numerous, furnished with a tuft of silky hairs. Trees and shrubs, bearing simple leaves without stipules, and amentaceous inflorescences (Figs. 470, 471).

The family contains only the two genera, *Salix*, Willow, and *Populus*, Poplar.

The flowers of the Willow (Fig. 470), unlike those of all the other *Amentaceae*, are pollinated by insects, not by the wind. They are accordingly provided with nectaries (the disc-scales) as a means of enticement, and the male flowers have an attractive odour, bright-coloured anthers, and a sticky pollen. Male and female catkins have essentially the same structure; they are beset with scale-like, entire bracts, in the axils of which the flowers are borne singly. Each male flower possesses usually two stamens (*Salix alba*), rarely three or more (*Salix triandra*, *S. pentandra*). The fruit is a two-valved capsule. The numerous seeds are disseminated by the wind; by means of their hairy appendages they are able to float for a long time in the air.

The Poplars (Fig. 471) are anemophilous. The flowers, accordingly, are destitute of nectaries. The catkins are similar to those of the Willow, but with toothed or lobed bracts. The fruit and seeds are like those of the Willow.

GEOGRAPHICAL DISTRIBUTION.—The *Salicaceae* inhabit almost exclusively the temperate and colder zones, where they are often abundantly represented, constituting an important part of the vegetation. They are especially characteristic of the low ground along the banks of streams, where the more shrubby Willows (*S. purpurea*, *triandra*, *viminalis*, etc.) form thicket-like growths, often overtopped by arborescent species (*S. alba*, *fragilis*). The Weeping Willow (*S. babylonica*) is indigenous to the East.

To the genus *Populus* belong, among others, the White Poplar (*P. alba*), the Black Poplar (*P. nigra*), the Aspen (*P. tremula*, Fig. 471), all natives of Europe, and the Lombardy Poplar (*P. pyramidalis*), originally indigenous to the East.

OFFICINAL.—*Salix alba*, *S. fragilis*, and other species yield CORTEX SALICIS.

Family **Cupuliferae.**—Flowers EPIGYNOUS, monœcious, with or without perigone; DISC ABSENT; ovary TWO- TO THREE-LOCULAR, WITH

ONE TO TWO SUSPENDED OVULES IN EACH LOCULUS; fruit, a one-seeded nut. Woody plants with SIMPLE, stipulate leaves; female inflorescences of different types (Figs. 472-478).

The *Cupuliferae* are deciduous, or, in the warmer zones, evergreen woody plants, with variously shaped, usually toothed or lobed leaves. Their flowers are small and inconspicuous; they are adapted to wind-pollination, and are accordingly destitute of any special means of attracting insects. The male flowers are either naked or have a perigone consisting of four to six members; the female flowers are variously constructed. The presence of a woody CUPULE is characteristic of many *Cupuliferae;* it consists of an involucre formed of coherent bracts investing the whole female inflorescence or only the single flowers, and completely enclosing the whole infructescence or the separate fruits, or only enveloping them at the base.

FIG. 472.—*Fagus silvatica.* 1, Flowering branch; 2, a male flower; 3, a female flower cut through longitudinally; 4, transverse section of ovary; 5, cupule and fruits; 6, fruit. (After WOSSIDLO.)

SUB-FAMILIES AND REPRESENTATIVE GENERA.—(1) *Betuloideae.* Ovary bilocular; no woody cupule. *Betula,* Birch; *Alnus,* Alder; *Corylus,* Hazel-nut; *Carpinus,* Hornbeam. (2) *Fagoideae.* Ovary with three, rarely with more loculi; cupule present. *Fagus,* Beech; *Quercus,* Oak; *Castanea,* Chestnut.

In the *Beech* (Fig. 472) the male flowers are borne in small, globose catkins, they have a bell-shaped, fringed perigone and numerous stamens. The female inflorescence is composed of two flowers with a six-leaved perigone and trimerous gynœcium. Each inflorescence gives rise to two three-sided nuts, which are invested by a woody cupule. The cupule is covered with hard bristles, and when ripe splits into four valves.

In the Chestnut (*Castanea vesca*) the fruit is also completely enclosed in a cupule until maturity; this is thickly covered with prickles, and splits into four valves when ripe.

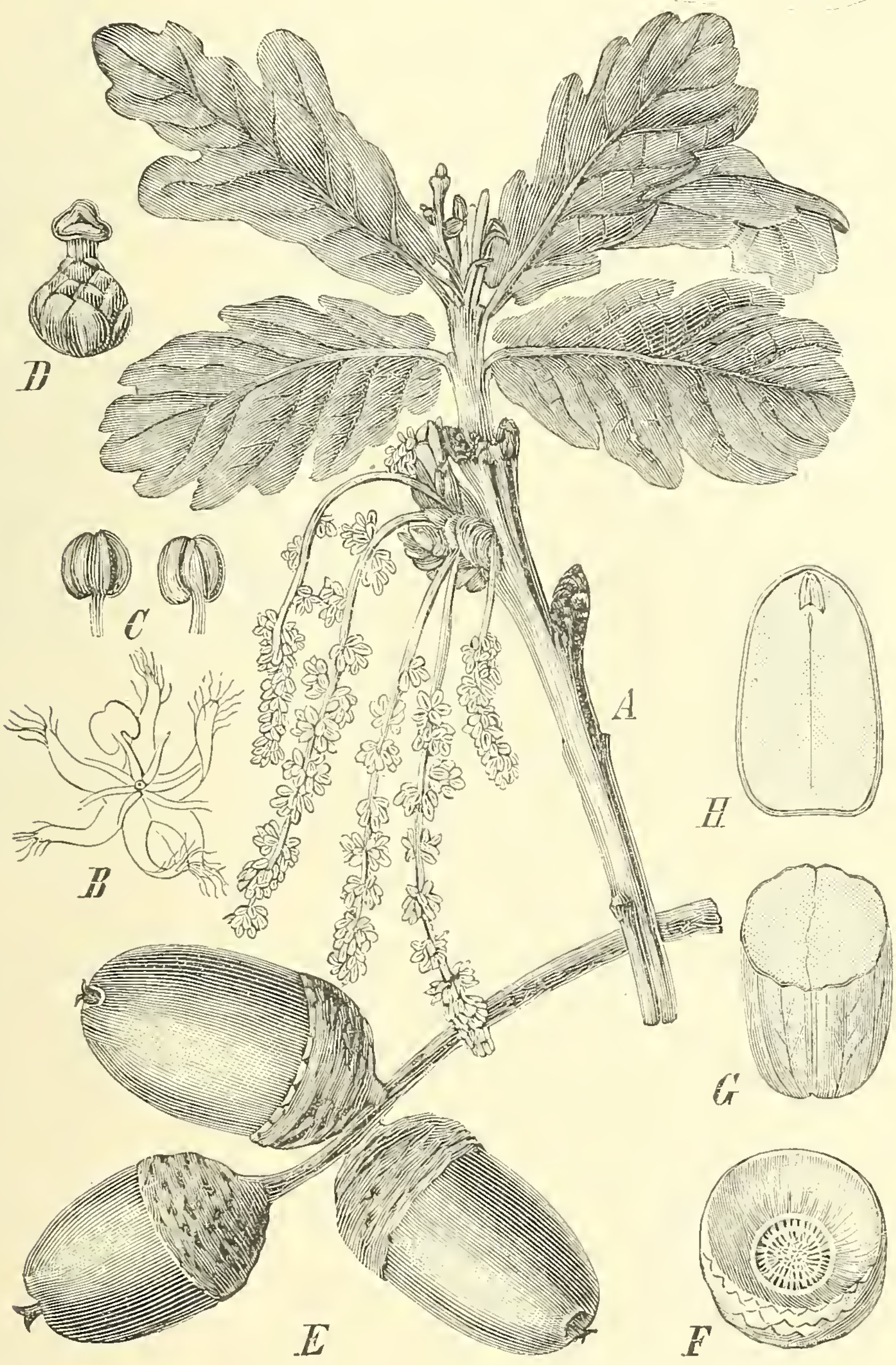


FIG. 473.—*Quercus pedunculata*. *A*, Flowering branch; *B*, a male flower (magnified); *C*, stamens (magnified); *D*, a female flower (magnified); *E*, infructescence; *F*, cupule; *G-H*, seed.—*OFFICINAL.*

The Oak (Figs. 473, 474) possesses long, slender male catkins with flowers disposed at intervals, and capitate or spike-like female inflorescences. Each female flower is provided with a scaly cupule, which ultimately invests the base of the solitary nut ("acorn"). Only two species are indigenous to Germany, *Q. pedunculata* and *Q. sessiliflora*, both of which are often regarded as varieties of the one species, *Q. robur*. In the first named the leaves have short stalks, and the female inflorescences are spicate ; in *Q. sessiliflora* the stalks of the leaves are long, while the female inflorescences are capitate.

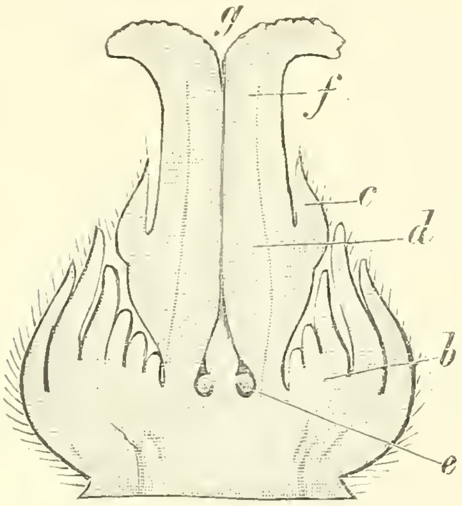


Fig. 474.—*Quercus pedunculata*, longitudinal section of the female flower. *b*, The young cupule ; *e*, ovule ; *d*, ovary ; *c*, perigone ; *f*, style ; *g*, stigma. (After Berg and Schmidt, magnified.)

The inflorescences of the Hazel (*e.g. Corylus Avellana*, the common Hazel-nut), unlike those of the genera just described, are developed in the preceding year; the male last over the winter, naked ; the female inflorescence is enclosed in a bud (Fig. 475). In early spring the male catkins elongate and produce an abundance of dry pollen, while the female inflorescences are distinguishable from the leaf-buds only by their larger size and projecting red stigmas. The nut is enveloped at the base by a sheath of succulent bracts.

In the Hornbeam, *Carpinus Betulus* (Fig. 476), the cylindrical loose inflorescences make their first appearance in the spring. The nut is provided with a three-lobed sheath.

The inflorescences of the Alder (*e.g. Alnus glutinosa*, Black Alder ; *A. incana*, Speckled or Hoary Alder), like those of the Hazel, are developed on the shoots of the previous year. The male are long and cylindrical; the female are much smaller, ovoid in shape, and form cone-like infructescences with two nuts at the base of each scale (Fig. 477).

In the Birch (*Betula alba*) the male inflorescences appear in autumn, the female not until the following spring ; both are cylindrical and many-flowered. The fruit is winged, and is borne in groups of three in the axil of each bracteal scale ; the scales become detached from the axis and fall off together with the fruit (Fig. 478).

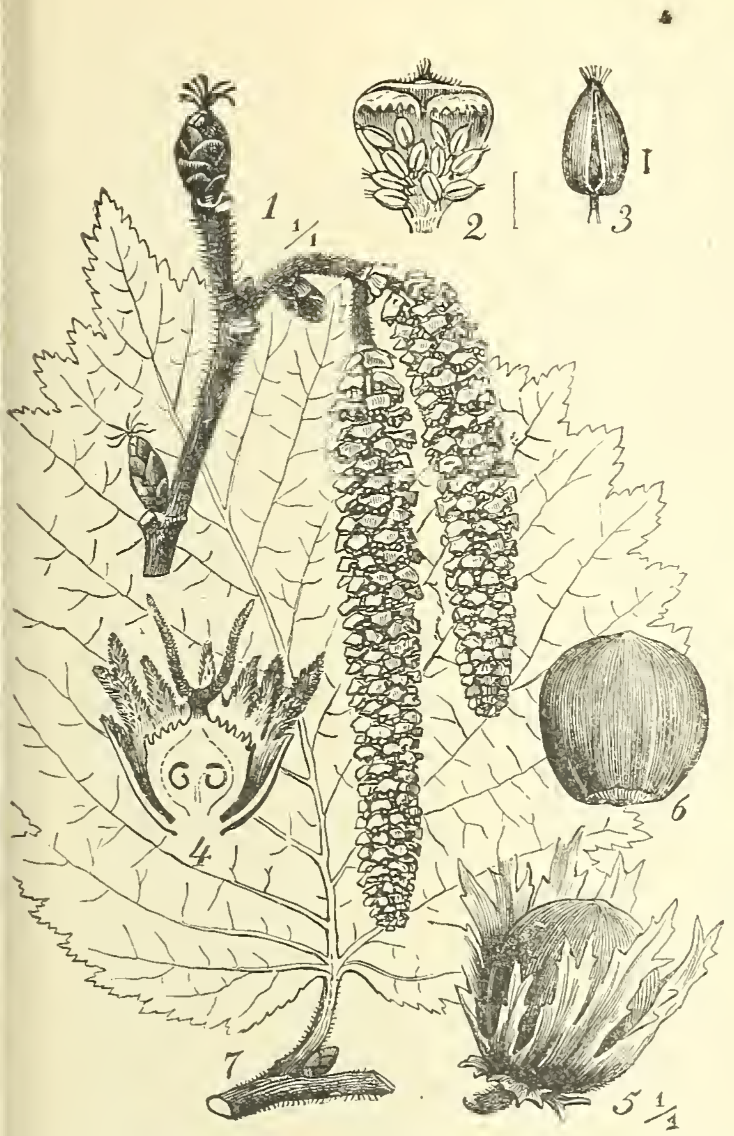
Geographical Distribution.—The *Cupuliferae* constitute the most important deciduous trees of the forests of the whole northern hemisphere, but only occur in the Tropics in the cooler mountainous regions.

This family supplies many plants of economic value. The wood of the Oak is particularly valuable on account of its hardness and density, while the bark is used for tanning, and the fruit as a cheap substitute for coffee. Cork is obtained from the Cork-Oak (*Quercus Suber* and *Q. occidentalis*) of Southern Europe and North Africa. The wood of the Beech is largely used for firewood, and from the seeds (Beech-nuts) oil is derived. The seeds of the Chestnut are edible.

Officinal.—The bark of some species of Oak, Cortex Quercus, and the acorns, Semen Quercus, are used medicinally. *Quercus infectoria*, indigenous to the East, produces, when stung by the Gall-fly, Cynips gallae tinctoriae, the officinal Gallae. *Fagus silvatica* gives Pix liquida. *Betula alba*, Oleum rusci s. betulinum.

Family **Juglandaceae.**—Flowers epigynous, monœcious, naked or with tetramerous perigone ; number of stamens indefinite ; ovary with two incomplete loculi, enclosing one erect ovule. Aromatic trees, usually having imparipinnate leaves without stipules.

In *Juglans regia*, the Walnut (Fig. 479), the thick, cylindrical male catkins are borne in the axils of the fallen leaves of the shoots of the previous year ; the two



ig. 475.—*Corylus Avellana.* 1, A flowering branch; 2, a male flower; 3, a stamen; 4, a female flower cut through longitudinally; 5, fruit with cupule; 6, fruit without cupule; 7, a foliage-leaf. (After Wossidlo.)

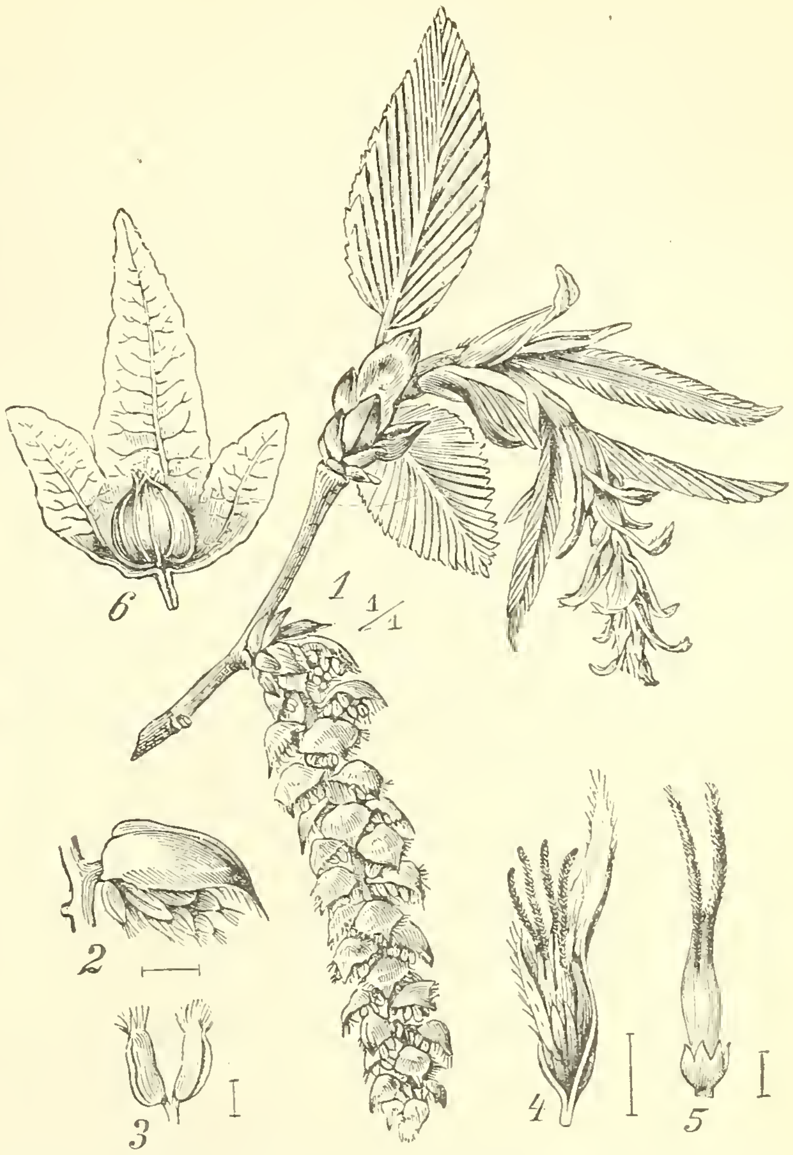
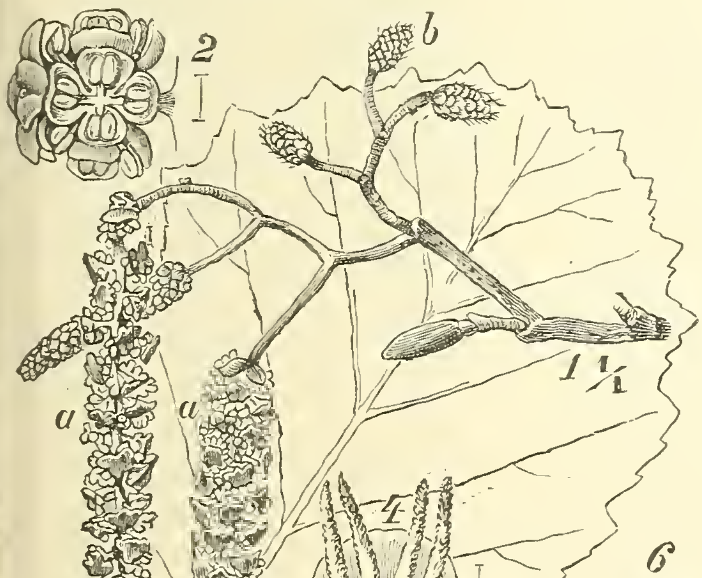


Fig. 476.—*Carpinus Betulus.* 1, Flowering branch; 2, a male flower; 3, stamens; 4, female flowers; 5, a female flower isolated. (After Wossidlo.)



ig. 477.—*Alnus glutinosa.* 1, Branch with male (*a*) and female (*b*) inflorescences; 2, male flowers; 3, female inflorescence; 4, two female flowers; 5, infructescence; 6, fruit. (After Wossidlo.)

Fig. 478.—*Betula alba.* 1, Branch with male (*a*) and female (*b*) inflorescences; 2, bract with three male flowers; 3, bract with three female flowers; 4, infructescence; 5, fruit. (After Wossidlo.)

bracteoles and the gamophyllous, tetramerous perigone are adherent and envelop a varying number of stamens. The female flowers are aggregated in few-flowered spikes at the apices of the leafy shoots of the same year. In the female flowers, as in the male, the leaves of the perigone are coherent and united with the bracteoles. The large, white papillose stigmas constitute the most conspicuous part of the flowers. The fruit is a drupe, and when ripe it has a brown, irregularly splitting exocarp and a hard endocarp. The seed, which is deeply lobed in consequence of the incomplete septation of the cavity of the ovary, consists of a thin seed-coat and two large, oily cotyledons attached to a short hypocotyl.

FIG. 479.—*Juglans regia.* Branch with male (*a*) and female (*b*) inflorescences; 2, a group of male flowers; *a*, stamen seen from the inner side; *b*, the same seen from the side; 3, a female flower; 4, the same in longitudinal section; 5, fruit, with pericarp partly removed; 6, the same in longitudinal section.—OFFICINAL. (After WOSSIDLO.)

GEOGRAPHICAL DISTRIBUTION.—The Walnut (*J. regia*) grows wild in Greece and Asia Minor. The other members of this small family are forest trees of North America and Eastern Asia. The wood of several species of *Juglandaceae*, particularly of the Walnut, is much used for furniture and in cabinet work.

OFFICINAL.—From *Juglans regia* is obtained FOLIA JUGLANDIS.

Family **Myricaceae.**—*Myrica gale* is a small shrub occurring on moors.

Family **Casuarinaceae.** — East Indian and Australian trees resembling *Equisetum* in habit.

Order 2. Urticinae

Flowers hypogynous, usually unisexual, small, with SIMPLE, CALYCOID PERIGONE; stamens opposite the leaves of the perigone, and of the same number; gynœcium one- to two-merous, in the last case one of the carpels usually REDUCED; ovary unilocular, with one ovule; seeds usually with endosperm. Herbs and woody plants with dense inflorescences.

There are no very essential differences between the *Amentaceae* and *Urticinae*. Inflorescences resembling the catkins of the *Amentaceae* sometimes occur in the *Urticinae*. The reduction of the gynœcium to a single fertile carpel does not always take place in the *Urticinae*, nor is an endosperm always present in the seeds without exception. In such cases, however, other characteristics and a comparison with allied forms leave no doubt of their proper position within this order.

FIG. 480.—*Ulmus campestris*. 1, Flowering branch; 2, branch with leaves; 3, a flower; 4, the same, cut through longitudinally; 5, fruit. (After WOSSIDLO.)

Some members of this family are herbs, others are shrubs or trees. They have variously shaped, but always stipulate leaves, and frequently they contain a latex. The flowers, as a rule, are wind-pollinated and inconspicuous; they are aggregated into thick inflorescences and produce great quantities of dry pollen, and have large, brush-like stigmas. Entomophilous forms adapted to insect-pollination occur in the *Moraceae* (*e.g.* the Fig). While in the *Amentaceae* the structure of the flowers is subject to great variation, in the *Urticinae* it is more uniform and constant. The almost invariable presence of a perigone, the haplostemonous stamens, the hermaphrodite or, by reduction, unisexual flowers are indicative of the high stage of development attained by this family. The fruit is either dry and nut-like or drupaceous.

Family **Ulmaceae.**—Flowers hermaphrodite or, as a result of suppression, unisexual, with four to six perigone leaves; stamens STRAIGHT in the bud; ovary dimerous, unilocular, with one SUSPENDED, ANATROPOUS ovule. Woody plants WITHOUT MILKY JUICE, with pinnately veined leaves and CADUCOUS stipules (Fig. 480).

This family comprises tall trees with two-ranked unsymmetrical, hairy leaves. The flowers are hermaphrodite and clustered in the axils of the leaves of the preceding year. The fruit is a winged nut.

GEOGRAPHICAL DISTRIBUTION.—The *Ulmaceae* are forest trees of the temperate and tropical zones. As examples of the genus *Ulmus* may be cited, *Ulmus campestris*, the Common Elm, and *U. effusa*, also the Witch-Hazel or Wych-Elm, *Ulmus montana*, all native of Europe. *Celtis australis*, from Southern Europe, and the Hackberry (*Celtis occidentalis*) from North America, both of which have drupaceous fruits, are frequently cultivated as ornamental trees.

Family **Moraceae.**—Flowers unisexual, usually with four perigone leaves; stamens STRAIGHT or INFLEXED in the bud; ovary dimerous, unilocular, with one SUSPENDED, ANATROPOUS ovule. Mostly trees or shrubs, rarely herbs, with milky juice and CADUCOUS stipules (Fig. 481).

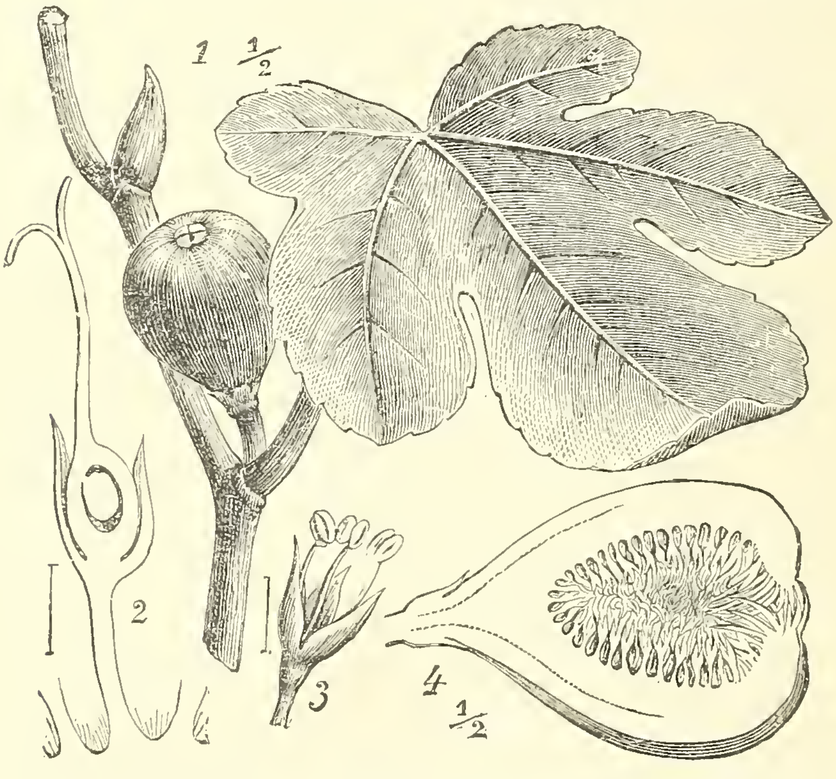


FIG. 481.—*Ficus carica*. 1, Flowering branch; 2, a female flower cut through longitudinally; 3, a male flower; 4, a fig in longitudinal section. (After WOSSIDLO.)

The *Moraceae* are easily distinguishable from the *Ulmaceae* by their latex tubes, and also by their peculiar inflorescences, frequently consisting of numerous axes which have become more or less coherent. Especially remarkable in this respect are the flowers and fruit of the Fig-tree, *Ficus carica* (Fig. 481). The fruit known as the Fig is the aggregated product of the complete union of the axes of a cymose inflorescence. The succulent part of the ripe fruit consists in its outer portions of the coherent axes, and internally of the perigones of the flowers comprising the inflorescence. The perigone of each flower encloses a hard nutlet, the whole representing a single fruit.

The *Moraceae* are represented in Germany only by cultivated species, the Mulberry tree, *Morus nigra*, which is of Asiatic origin, and by the Fig-tree, *Ficus carica*. The genus *Ficus* is the largest of the family, and is especially remarkable on account of the great variety of forms it assumes, the size and beauty of many of its species, and its economic value. The seed of the East Indian Banyan, *Ficus bengalensis*, germinates on the branches of other trees, to which it is carried by birds. Growing first as an epiphyte, it sends down slender roots to the ground, which develop ultimately into thick columns; the branching crown in the meantime becomes enormously expanded horizontally, and there is formed a large hall of columns, in the shade of which there is sufficient space for a village. The tree upon which the seed first germinated disappears entirely. The species of *Ficus* and the majority of the *Moraceae* occur in the virgin forests of tropical countries.

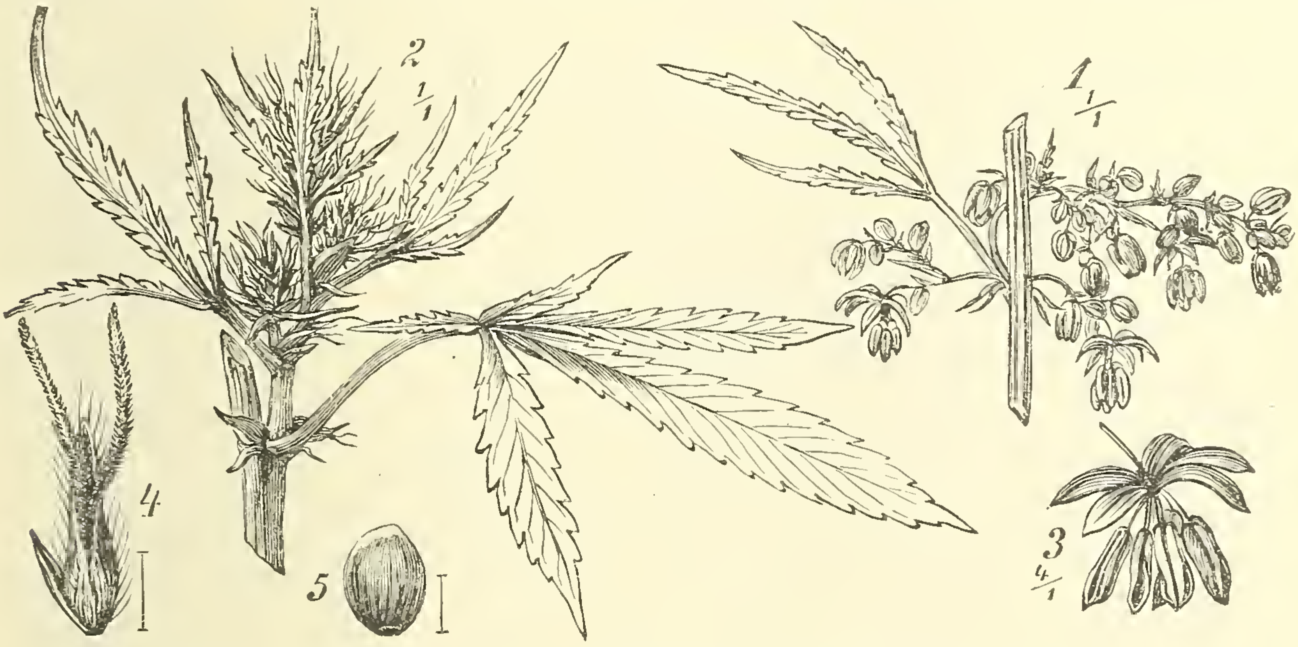


FIG. 482.—*Cannabis sativa*. 1, Part of a flowering shoot of a male plant; 2, the same of a female plant; 3, a male flower; 4, a female flower; 5, fruit. (After WOSSIDLO.)

Caoutchouc is obtained from the latex of many species of *Moraceae;* other species have edible fruit, *e.g.* the Mulberry, Fig, and the Bread-fruit tree, *Artocarpus incisa*.

OFFICINAL.—From *Morus nigra* is derived SYRUPUS MORI; *Ficus elastica* (East Indies), *Castilloa elastica* (Mexico), and other tropical *Moraceae* afford CAOUTCHOUC.

Family **Cannabinaceae.**—Flowers typically diœcious; the male with five perigone leaves, and as many stamens with STRAIGHT filaments in the bud; the female flower has an entire, cup-like perigone. Ovary dimerous, with one SUSPENDED, ANATROPOUS ovule. Herbs WITHOUT LATEX, with palmately-nerved leaves and PERSISTENT stipules (Figs. 482, 483).

GENERA.—*Cannabis*, *Humulus*. *Cannabis sativa*, Hemp, is a native of the East Indies. It is an annual herb with palmately divided leaves beset with stiff hairs. The male flowers form a large, profusely branched panicle with leaves only at the base. The female flowers are aggregated into small spikes, and are concealed by numerous leaves; as in most cases of wind-pollination, the stigmas are characteristically large and papillose (Fig. 482). The female plants are larger and possess thicker foliage than the male. The subtending leaves of the female flowers of the variety *indica* are covered with glandular hairs, which excrete resin. The fruit is a nut with a seed containing much oil.

The Hop, *Humulus Lupulus* (Fig. 483), is both cultivated and found wild. It is a twining, perennial herb with hispid, palmately-lobed leaves. The male flowers are united in profusely branched, axillary panicles devoid of leaves; the female are clustered into cone-like inflorescences, whose scales represent, in part, the stipules of undeveloped hypsophylls, in part the subtending leaves of the flowers. When ripe, the scales are covered with yellow glandular hairs which secrete lupulin. It is to the presence of this lupulin that the value of hops in brewing is due.

Officinal. — *Cannabis sativa* provides Fructus Cannabis; from *Cannabis sativa* var. *indica* is obtained Herba Cannabis indicae. The glands of the cone-scales of *Humulus Lupulus* have an officinal value as Lupulinum or Glandulae lupuli, the whole cone as Strobilus lupuli.

Fig. 483.—*Humulus Lupulus.* 1, Branch of male inflorescence; 2, branch with female inflorescences; 3, a female inflorescence; 4, two female flowers with bract; 5, infructescence; 6, fruit. (After Wossidlo.)

Family **Urticaceae.**—Flowers unisexual through reduction, usually with four-leaved perigone and with stamens INFLEXED in the bud; ovary MONOMEROUS, WITH AN ERECT, ATROPOUS OVULE. Herbs and shrubs WITHOUT LATEX, with stipulate leaves (Fig. 484).

The *Urticaceae* are mostly herbs and shrubs with simple leaves, which are often armed with stinging hairs (Fig. 115). The flowers are restricted to wind-pollination, and are clustered in thick, greenish or whitish inflorescences. The fruit is a nut or a drupe.

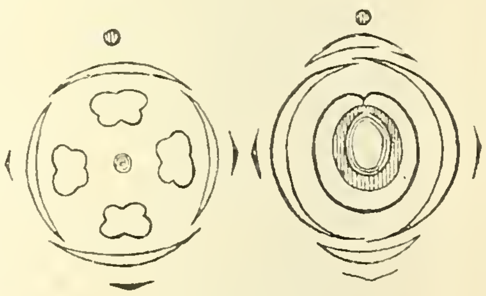


Fig. 484.—Floral diagram of *Urtica dioica.* *A*, the male; *B*, the female flower. (After Eichler.)

Geographical Distribution.—The Stinging Nettles, *Urtica urens* and *dioica*, occur everywhere as common weeds. The majority of the representatives of this family, however, inhabit the warmer zones, where they constitute a considerable proportion of the herbaceous and shrubby vegetation of the primitive forests.

Order 3. Polygoninae

Flowers hypogynous, HERMAPHRODITE, sometimes unisexual by suppression, generally TRIMEROUS; perianth ABSENT OR DEVELOPED AS A PERIGONE; ovary UNILOCULAR, WITH A SINGLE BASAL ATROPOUS OVULE.

The *Polygoninae* occupy an intermediate position between the *Urticinae* and the following order, *Centrospermae*. They differ from the *Centrospermae* in having atropous ovules and in the trimerous structure of their flowers.

The members of this order are mostly herbs, rarely small woody plants. They generally have axes swollen at the nodes, simple, usually entire leaves, and spike-like inflorescences with closely-crowded small flowers. The flowers themselves vary greatly in structure; sometimes naked, and of the simplest structure; sometimes, by the dissimilarity of the outer and inner leaves of the perigone, and by the possession of two whorls of stamens, they exhibit a higher stage of development than is attained by the *Urticinae*. In this and all the orders which follow, the pollen-tube enters the ovule by means of the micropyle. The fruit is either a nut or drupaceous in character; the seeds contain a mealy albumen.

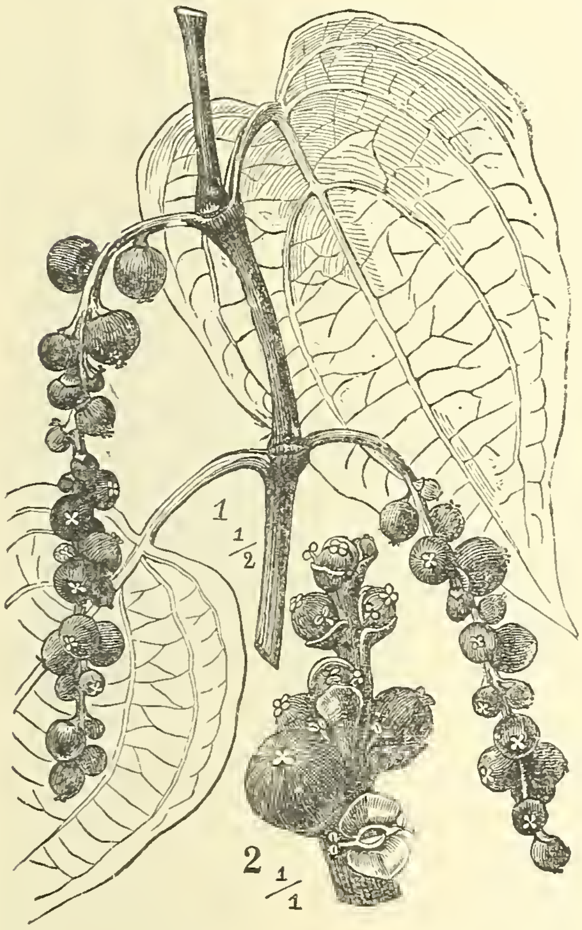


FIG. 485.—*Piper nigrum*. 1, Part of shoot with young infructescences; 2, tip of fruit-spike. (After WOSSIDLO.)

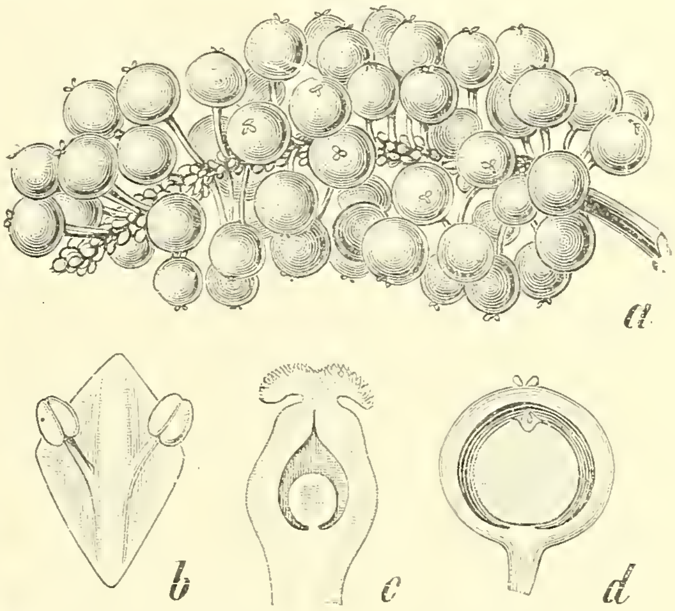


FIG. 486.—*Piper Cubeba*. *a*, Infructescence; *b*, a male flower; *c*, a female flower in longitudinal section; *d*, fruit in longitudinal section.—*OFFICINAL*. (After BERG and SCHMIDT. *a*, Nat. size; *b*, *c*, *d*, magnified.)

Family **Piperaceae.**—Flowers NAKED, typically trimerous, but usually REDUCED; fruit DRUPACEOUS; seeds with PERISPERM. Herbs and shrubs with stipulate or exstipulate leaves (Figs. 485, 486).

The *Piperaceae* are found exclusively in tropical countries, where, as herbs and shrubs, often climbing by means of roots or living as epiphytes with inconspicuous, densely clustered, green flower-spikes, they constitute an essential though not particularly prominent part of the Flora. *Piper nigrum* L., the Black Pepper, is a shrubby root-climber native of the East Indies, and is now cultivated in all tropical countries. The unripe drupes of this species are familiarly known as black pepper ; white pepper consists of the kernels of the fruit of the same plant, freed from the exocarp. The perisperm is large and mealy.

OFFICINAL.—The dried, unripe fruit of *Piper Cubeba*, a climbing shrub of the Sunda Islands, is the officinal CUBEBA. It is distinguishable from pepper-corns by the presence of a stalk-like appendage (Fig. 486).

Family **Polygonaceae** (30).—Flowers with single or double perigone, typically trimerous, but the number of stamens is frequently increased by division ; fruit almost always a nut ; seeds WITHOUT PERISPERM. Herbs, rarely woody plants, especially characterised by alternate leaves and connate stipules in the form of TUBULAR SHEATHS (Ochrea, Figs. 487-489).

The wild or cultivated *Polygonaceae* are herbs with hollow stems and simple, rarely lobed, alternate leaves. The OCHREA, formed by the coherent stipules, is very characteristic ; it first encloses the apex of the shoot, and afterwards surrounds the base of the internode and axillary bud as a scaly tube. The flowers are small and aggregated into compound spikes, racemes, or panicles ; they have a calycoid or corollaceous, reddish perigone, according as they are anemophilous or entomophilous. The inner circle of stamens is often suppressed (*Rumex*). The fruit is in most cases a three-sided, thin-walled nut with a mealy endosperm.

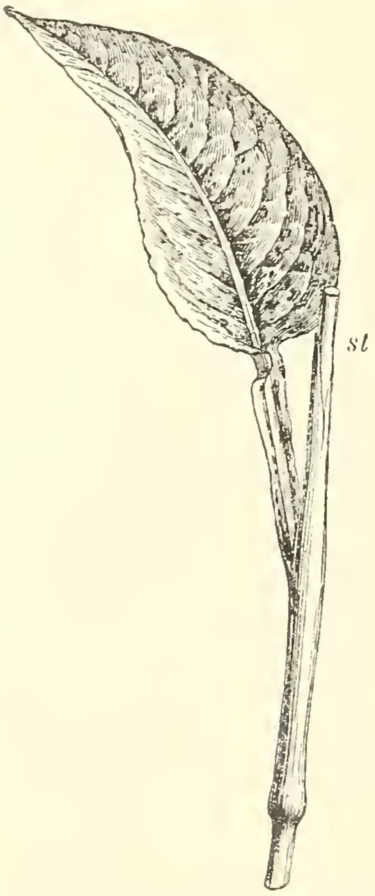


FIG. 487.—Leaf of *Polygonum lapathifolium*. *st*, ochrea. (Reduced. After DUCHARTRE.)

Polygonum, Knot-Grass, has a corollaceous, five-leaved perigone and five to eight stamens. *Rumex*, the Dock or Sorrel, possesses a six-leaved (3 + 3) calycoid perigone and six (6 + 0) stamens. *Rheum*, Rhubarb, has also a calycoid perigone and nine (6 + 3) stamens.

GEOGRAPHICAL DISTRIBUTION.—The *Polygonaceae* are chiefly found in the North Temperate Zone. *Rumex acetosa*, Sorrel, contains a large amount of potassium oxalate, and is on that account esteemed as a vegetable and often cultivated for that purpose. Other frequently cultivated plants belonging to this family are the Buckwheat, *Fagopyrum esculentum*, and the different species of garden Rhubarbs.

OFFICINAL.—The rhizome of *Rheum officinale* and *R. palmatum* is the officinal RADIX RHEI.

FIG. 488.—*Rheum officinale*, greatly reduced. (After BAILLON.)

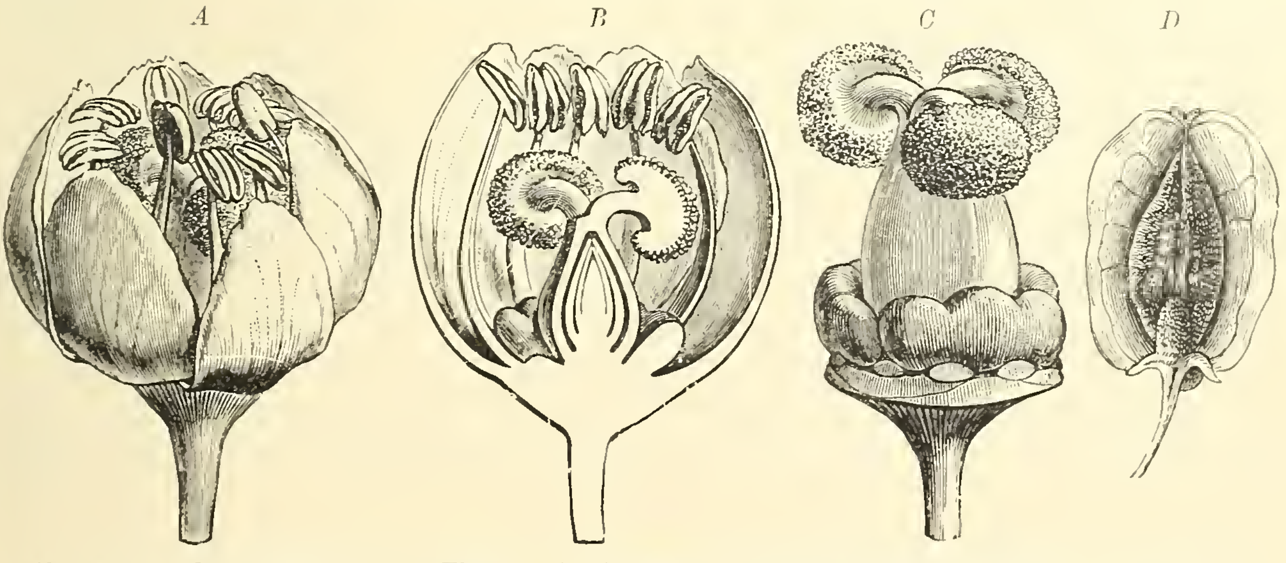


FIG. 489.—*Rheum officinale*. *A*, Flower; *B*, the same cut through longitudinally; *C*, gynœcium with disc; *Rheum compactum*, *D*, fruit. (After LÜRSSEN, magnified.)

Order 4. Centrospermae

Flowers hermaphrodite, usually hypogynous, PENTAMEROUS with CALYCOID PERIGONE, OR WITH CALYX AND COROLLA, rarely naked; andrœcium haplostemonous or diplostemonous; ovary commonly UNILOCULAR, WITH A SINGLE, BASAL OVULE, or with a FREE-CENTRAL PLACENTA and numerous CAMPYLOTROPOUS ovules; seeds with perisperm and a CURVED embryo.

The *Centrospermae* are for the most part herbaceous, rarely woody plants with simple, exstipulate leaves. The flowers are either inconspicuous, white, or highly coloured, according to the method of pollination. As regards their structure, the flowers of the different members of this order may be arranged in an ascending series, beginning with the simplest forms, resembling those of the *Urticaceae* and gradually advancing to the more highly developed, constructed after the pentacyclic, pentamerous type, characteristic of the Dicotyledons, and having a perianth differentiated into calyx and corolla. THE CENTROSPERMAE THUS LINK TOGETHER THE APETALOUS AND COROLLATE DICOTYLEDONS. The unilocular character of the ovaries in most members of this order is due, no doubt, to the disappearance of the dissepiments, as in some cases they are partly retained (Fig. 491).

In the simplest cases the flowers consist typically of three whorls (*e.g. Chenopodiaceae*); the number of the whorls is in other instances increased to five (*e.g.* most *Caryophyllaceae*), but in other cases it is reduced again, by suppression, to three (*e.g.* the Caryophyllaceous *Paronychioideae*). At the end of the series, accordingly, flowers occur with a structure apparently similar to those at the beginning; but in the reduced flowers one may often distinguish traces of the suppressed whorls, which are not in any way represented in the more simple, tricyclic types.

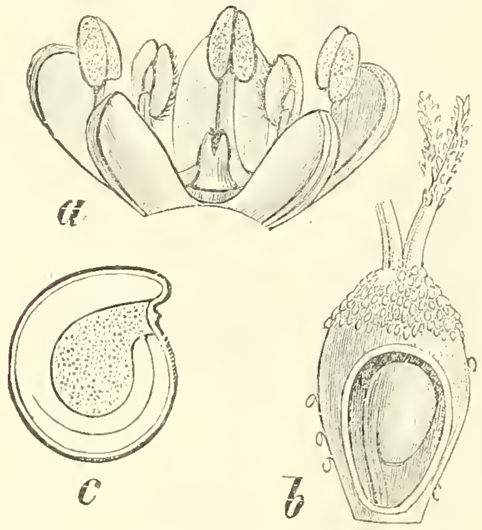


FIG. 490.—*a*, Flower of *Beta vulgaris*; *b*, gynœcium of *Chenopodium multifidum*, with part of wall of ovary removed; *c*, seed of *Beta vulgaris*. (After VOLCKENS in *Natürl. Pflanzenfamilien*, magnified.)

Family **Chenopodiaceae.** — Flowers usually WITHOUT BRACTEOLES, with a single calycoid PERIGONE; andrœcium HAPLOSTEMONOUS, EPIPETALOUS; ovary two- to five-merous, with ONE OVULE. Fruit generally a nut (Fig. 490).

The *Chenopodiaceae* are herbs and small woody plants, with scattered, often fleshy, leaves, and greenish inflorescences of small, clustered flowers. The flowers are often unisexual in consequence of suppression. The nutlets are filled with a mealy albumen.

Chenopodium, Goosefoot or Pigweed, hermaphrodite, with greenish, and after flowering, dry perianth; *Blitum*, with succulent perianth when the fruit is ripe;

Atriplex, Orache, monœcious, with naked female flowers; *Beta*, Beet, epigynous; *Spinacia*, Spinach, diœcious, the perianth hardening during the ripening of the fruit and adhering to the nut.

GEOGRAPHICAL DISTRIBUTION.—The *Chenopodiaceae* are for the most part saline plants, and chiefly occur near the ocean or in deserts and steppes. In such situations they are usually developed as succulent and not infrequently prickly herbs or woody plants. The most important cultivated species of this family are the Spinach, *Spinacia oleracea*, and the different varieties of the common Beet, *Beta vulgaris*, of which the most important is the Sugar-Beet, *B. altissima*. *Beta vulgaris* has itself probably been derived by culture from *B. maritima*, growing wild on the coast of the Mediterranean.

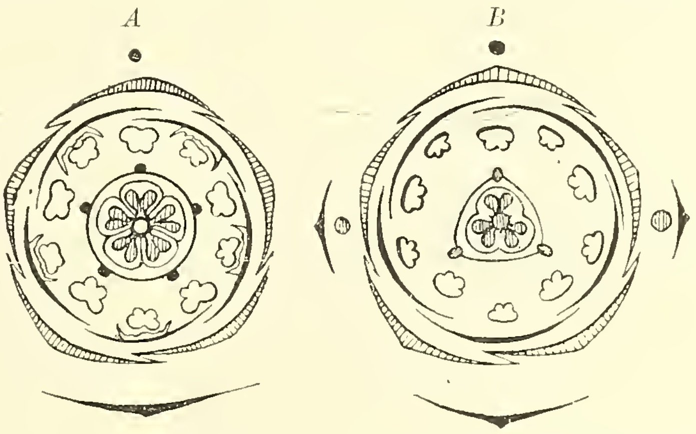


FIG. 491.—Diagrams of the *Caryophyllaceae*. *A*, *Viscaria*, lateral walls present in the lower part of the ovary; *B*, *Silene*, lateral walls absent. (After EICHLER.)

OFFICINAL.—*Beta vulgaris* var. *rapa* yields cane-sugar, SACCHARUM. *Chenopodium ambrosioides* (an annual herb from tropical America, cultivated in Europe) yields HERBA CHENOPODII.

Family **Amarantaceae.**—Flowers with two large bracteoles, and dry, often highly coloured, perigone; in other respects resembling the preceding family, *Amarantus*.

Family **Caryophyllaceae.**—Flowers with CALYX and COROLLA, the latter sometimes suppressed; andrœcium DIPLOSTEMONOUS or, by

FIG. 492.—*Melandryum album*. 1, Inflorescence; 2, a male flower; 3, a female flower; 4, fruit; 5, seed. (After WOSSIDLO.)

reduction, haplostemonous. Ovary rarely with only one ovule, more frequently WITH NUMEROUS OVULES. Fruit usually a capsule (Figs. 491-493).

The *Caryophyllaceae* are herbs, rarely shrubs, of varied appearance. They have opposite, entire, frequently narrow leaves and dichasial inflorescences. The flowers in some genera are small and of a greenish colour, but are usually provided with a white or brightly-coloured corolla, and are frequently large and conspicuous. In many cases all the floral whorls are pentamerous, but commonly the gynœcium is two- to three-merous. The capsules split at the apex into valves or teeth; in a few cases the fruit is a nut or berry.

FIG. 493.—*Agrostemma Githago* ($\frac{2}{3}$ nat. size).—POISONOUS.

SUB-FAMILIES AND REPRESENTATIVE GENERA.—(1) *Alsinoideae:* calyx polysepalous; petals with short claws; fruit a capsule. *Cerastium,* Chickweed, flowers entirely pentamerous. *Spergula,* Spurrey, and *Stellaria,* Starwort or Stitchwort, with trimerous ovaries and cleft petals. *Arenaria,* Sandwort, distinguished from *Stellaria* by its entire petals. (2) *Paronychioideae:* calyx polysepalous; corolla wanting or reduced; ovary with one ovule; fruit a nut. *Scleranthus,* Knawel; *Herniaria.* (3) *Silenoideae:* calyx gamosepalous; petals with long claws; fruit a capsule. *Lychnis,* Campion, with pentamerous ovary; *Silene,* with trimerous ovary and six-toothed capsule. *Dianthus,* Pink, with trimerous ovary and four-toothed capsule. The flowers of this group often have ligular appendages to the petals at the throat of the corolla.

GEOGRAPHICAL DISTRIBUTION.—The *Caryophyllaceae* are cosmopolitan in their geographical range, but they prefer the temperate and colder zones, where they are represented by numerous species growing in the most varied situations.

POISONOUS.—*Agrostemma Githago,* Corn-Cockle (Fig. 493), a hairy weed, reaching a height of 80 cm., common in grain-fields, with narrow leaves, violet-coloured flowers, and many-seeded capsules. The seeds when abundantly mixed with the grain give the flour toxic properties. *Saponaria officinalis,* the common Soapwort or Bouncing Bet, a stout perennial with clustered, rose-coloured flowers. The saponin contained in all parts of the plant renders it somewhat poisonous.

Officinal.—*Herniaria glabra* and *hirsuta*, Herba Herniariae.

Order 5. Polycarpicae

Flowers hypogynous or perigynous, hermaphrodite, partly or wholly SPIRAL, with NUMEROUS stamens and FREE CARPELS; seeds with endosperm.

This order comprises herbs and woody plants of very different appearance, their relationship being only revealed by the structure of the flowers. The type is most accurately represented in such forms as have at least an acyclic andrœcium and gynœcium, with numerous stamens and carpels inserted on a convex axis (Fig. 494). Flowers constructed in this manner are the rule in the *Ranunculaceae*, *Magnoliaceae*, and *Anonaceae*. These three large families form a central group about which the families with flowers less typically developed may be arranged. The most uniform characteristic of the whole order is the apocarpous gynœcium, although in the *Nymphaeaceae*, in some *Ranunculaceae*, and also in the *Lauraceae*, the systematic position of which is somewhat uncertain, the carpels are more or less united.

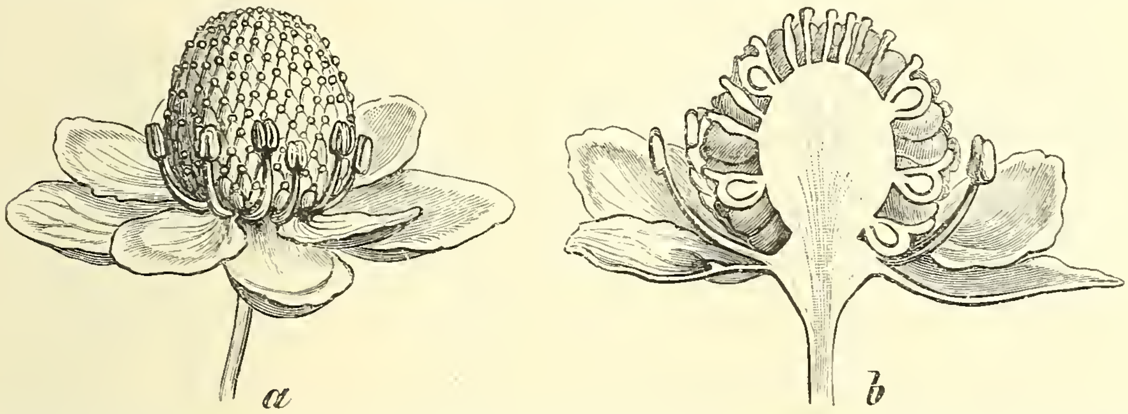


Fig. 494.—Flower of *Ranunculus sceleratus*; *b*, the same, cut through longitudinally; magnified. (After Baillon.)

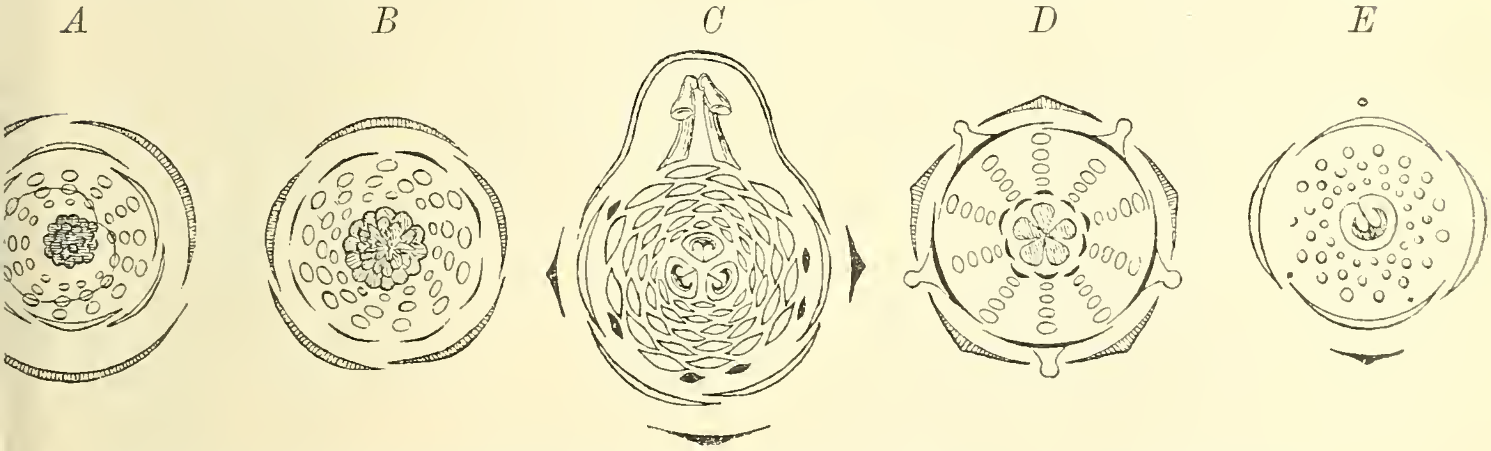


Fig. 495.—Floral diagrams of *Ranunculaceae*. *A*, *Anemone nemorosa*. *B*, *Adonis autumnalis*. *C*, *Aconitum napellus*. *D*, *Aquilegia vulgaris*. *E*, *Cimicifuga racemosa*. (After Eichler.)

FIG. 496.—*Helleborus foetidus* (⅛ nat. size).
POISONOUS.

FIG. 497.—*Aconitum Lycoctonum* (½ nat. size).—*POISONO*

FIG. 498.—*Caltha palustris.*—*POISONOUS.*

FIG. 499.—*Aconitum Napellus* (½ nat. size).—*POISONOU*
and *OFFICINAL.*

The convex flower-axis, the spiral arrangement of the parts, the numerous stamens, are usual, if less constant, characteristics of this order. There are included in the *Polycarpicae*, as is frequently the case in other orders, isolated groups which do not exhibit a single one of the distinctive characteristics of the order, but which, nevertheless, show such marked affinity to other undoubtedly typical groups, that they must be regarded as belonging to the same general alliance.

Fig. 500.—*Ranunculus sceleratus* (½ nat. size.)
Poisonous.

Fig. 501.—*Anemone Pulsatilla* (½ nat. size.)
Poisonous.

The order in which the different families are named is not intended to be indicative of their relative position with regard to each other, in an ascending series. Linked to the *Ranunculaceae*, on the one side, are the *Nymphaeaceae* and *Ceratophyllaceae*, and on the other the *Magnoliaceae* and allied families; while the *Berberidaceae*, *Menispermaceae*, and perhaps also the *Lauraceae*, form a separate subordinate alliance within the order.

Family **Ranunculaceae.**—Flowers HYPOGYNOUS, usually actinomorphic; very rarely cyclic, usually ACYCLIC throughout or so at least in the andrœcium and gynœcium; perianth single or double, in the last case frequently with corollaceous calyx and petals abnormally developed, most commonly as nectaries; stamens indefinite, USUALLY NUMEROUS; pollen-grains with TWO TO THREE PORES; carpels in INDEFINITE, OFTEN LARGE, NUMBERS, usually FREE; seeds with albumen. Herbs, rarely woody plants, with alternate leaves WITHOUT OIL-GLANDS (Figs. 494-505).

FIG. 502.—*Hydrastis canadensis.* ¼ natural size. OFFICINAL (*Nat. Pflanzenfamilien*, iii.2).

Most *Ranunculaceae* are medium-sized herbs, frequently with a radical rosette of deeply-lobed leaves and sparingly-leaved fertile shoots. The flowers are usually conspicuous, often solitary, and then terminal or axillary, or sometimes aggregated, in loose, and more rarely compact, racemose or cymose inflorescences. Insect-pollination is general, and has produced corresponding adaptations to it in the flowers, such as the bright colour of the perianth, or when it is reduced as in the species of *Thalictrum*, of the andrœcium, and the development of nectaries (Fig. 503, 2). The nectaries are developed either as small depressions at the base of the petals (*Ranunculus*), or the whole petal is transformed into a cup-shaped nectary (*Helleborus*, *Aconitum*).

The carpels of the *Ranunculaceae* are converted at maturity into capsules (*Helleborus*, *Aconitum*, Fig. 504), or as in *Ranunculus* (Fig. 505) and *Anemone*, into nutlets or achenes, frequently having long, feathery appendages (*Clematis*, *Pulsatilla*, Fig. 501), or, less frequently, into berries (*Actaea*, *Hydrastis*).

REPRESENTATIVE GENERA.—With CAPSULES: *Nigella*, carpels syncarpous; *Paeonia*, *Caltha*, with corollaceous calyx and no corolla; *Aquilegia* (Columbine), flowers cyclic, with spurred petals; *Aconitum* (see under Poisonous); *Delphinium* (Larkspur), flowers zygomorphic, one sepal with long spur. With NUTLETS: *Ranunculus* (Crowfoot, Buttercup), with green calyx and usually with yellow corolla, petals with nectaries; *Adonis*, *Anemone*, with single corollaceous perigone; *Thalictrum* (Meadow-Rue), with small, greenish perigone and long stamens; *Clematis*, climbing plants with opposite leaves, flowers with single, corollaceous perigone.

GEOGRAPHICAL DISTRIBUTION.—The *Ranunculaceae* are represented chiefly in the North Temperate Zone. Many are favourite ornamental plants, especially different species of *Paeonia*, *Clematis*, *Aquilegia*, *Nigella*, *Adonis*, and the Christmas-Rose, *Helleborus niger*.

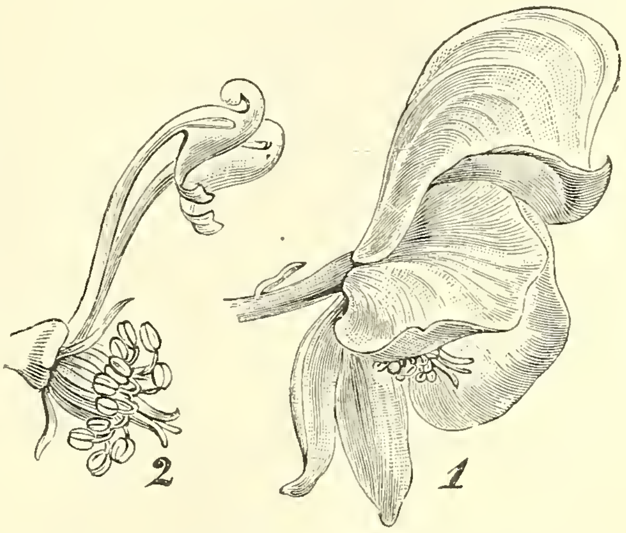


FIG. 503.—1, Flower of *Aconitum Napellus*; 2, nectaries, androecium and gynoecium of the same. (After WOSSIDLO.)

POISONOUS.—The whole family is extraordinarily rich in toxic principles, which are so abundant in many species as to render them dangerously poisonous. The following may be cited as the most poisonous plants of the *Ranunculaceae*.

All the species of *Aconitum*, in particular *A. Napellus* and *A. Lycoctonum*. The former (Fig. 499) is a perennial plant with tubers, one of which dies in the autumn, while the other, as in the *Orchidaceae*, gives rise to a new plant in the succeeding spring. The flowers are distinctly zygomorphic (Fig. 503). One of the five dark violet sepals is helmet-shaped; two of the petals are transformed into hood-shaped nectaries raised on long claws, while the others are reduced to filamentous rudiments; the numerous stamens surround three apocarpous carpels, each of which produces a follicle at maturity. *Aconitum Lycoctonum* (Fig. 497) has smaller yellow flowers, and, instead of tubers, a slender rhizome. *A. variegatum* and *A. Stoerckeanum*, allied to *A. Napellus*, are also extremely poisonous.

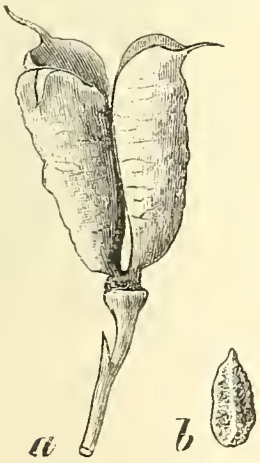


FIG. 504.—*Aconitum Napellus*. *a*, Fruit (nat. size); *b*, seed (× 2).

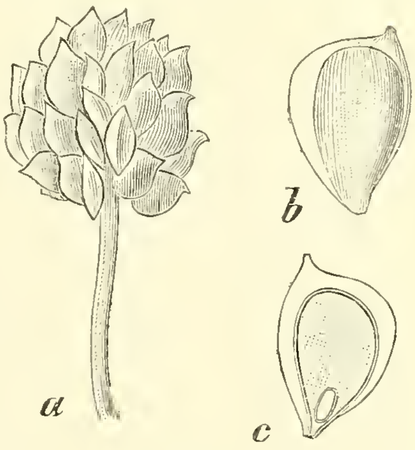


FIG. 505.—*a*, Apocarpous fruit of *Ranunculus acris* (× 2½); *b*, a carpel; *c*, the same in longitudinal section (*b*, *c*, × 4).

All the species of *Ranunculus* are also more or less poisonous. *R. sceleratus*, Celery-leaved Crowfoot, probably one of the most noxious species, is a glabrous herb with three-lobed, somewhat fleshy leaves and small light yellow flowers (Fig. 500). The Tall Crowfoot or Buttercup, *R. acris,* is the frequent cause of poisoning in cattle. It has a hairy stem, palmately divided leaves and bright yellow flowers. The Marsh Marigold, *Caltha palustris* (Fig. 498), though less poisonous, is a source of danger to children on account of its frequency and attractive flowers. *Helleborus foetidus,* Bear's Foot (Fig. 496), a large glabrous perennial, has palmately divided leaves and yellowish green, somewhat bell-shaped, flowers with numerous stamens and few carpels. The perianth consists of a large-leaved calyx and conical honey-leaves ; the carpels when ripe become follicles. Both the Green Hellebore, *H. viridis,* and the Christmas-Rose or Black Hellebore, *H. niger* (with reddish white flowers), are also poisonous. Species of *Adonis* (*e.g. A. vernalis*), *Anemone* (in particular *A. nemorosa,* and even more so *A. Pulsatilla* (Fig. 501), *Clematis* and *Delphinium* (especially *D. Staphysagria*) are also poisonous, but in a less degree.

FIG. 506.—*Myristica fragrans.* Flowering shoot. Ripe fruits dehiscing and after the removal of one valve of the capsule.—*OFFICINAL.* (After BERG and SCHMIDT.)

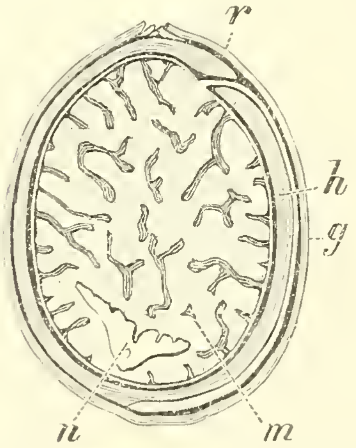


FIG. 507.—*Myristica moschata,* seed, cut through longitudinally; *g,* aril; *h,* outer integument, interrupted at *r* by the raphe ; *m,* albumen ; *n,* embyro (nat. size).—*OFFICINAL.* (After BERG and SCHMIDT.)

OFFICINAL.—*Aconitum Napellus* yields TUBERA v. RAD. ACONITI and FOLIUM ACONITI. *Hydrastis canadensis* (North America) yields RHIZ. s. RAD. HYDRASTIS and HYDRASTINUM.

Family **Magnoliaceae.**—Flowers as in the *Ranunculaceae,* but the pollen-grains have only ONE GERM-PORE. Woody plants with OIL-CELLS. Tropical and temperate

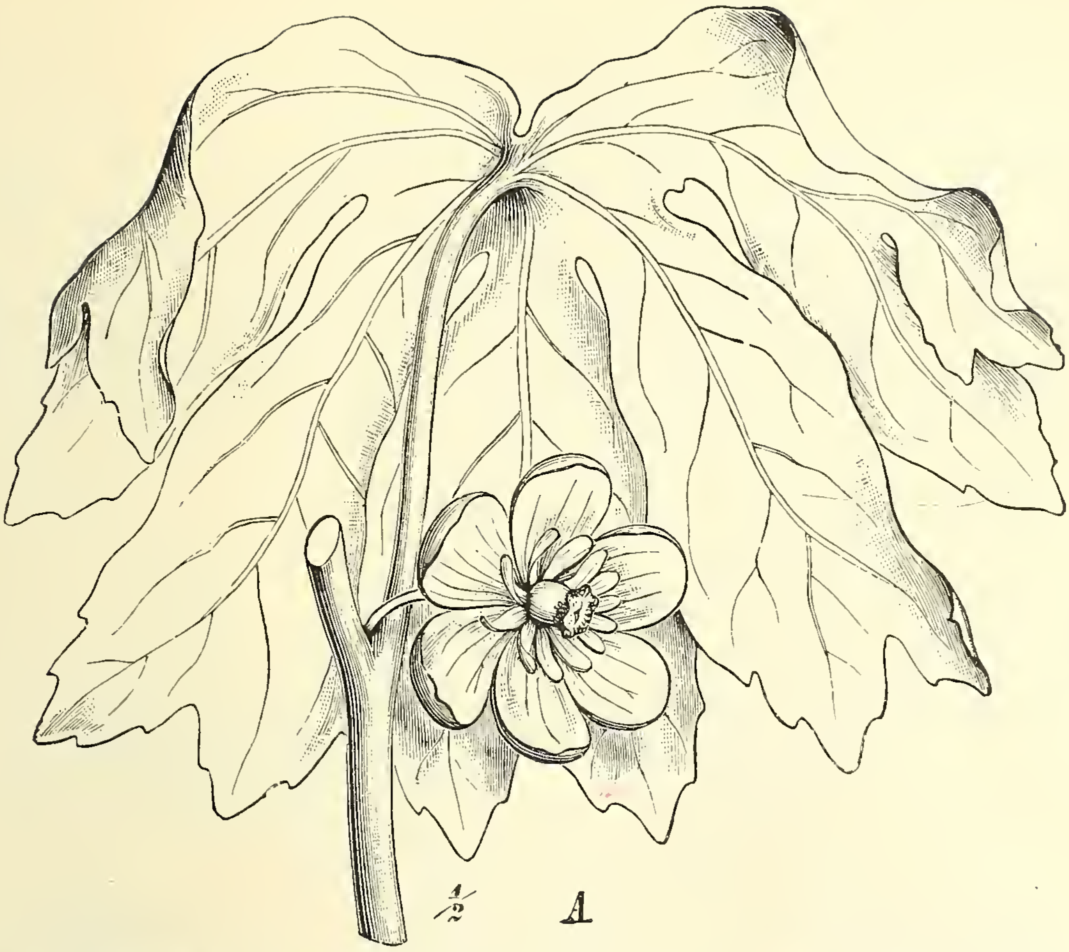


FIG. 508.—*Podophyllum peltatum* (½ nat. size).—*OFFICINAL.* (From *Nat. Pflanzenfamilien*, iii.₂.)

FIG. 509.—*Jatrorrhiza peltata* (½ nat. size).—*OFFICINAL.* (After BERG and SCHMIDT.)

Asia and North America. *Magnolia; Liriodendron,* Tulip-tree. OFFICINAL: FRUCTUS ANISI STELLATI from *Illicium anisatum.* The false star anise from *I. religiosum* is poisonous.

Family **Myristicaceae** (^{31}).—Tropical forest-trees. Seeds provided with arillus (Figs. 506, 507). OFFICINAL: *Myristica fragrans* (Moluccas). The seed of the Nutmeg is SEMEN MYRISTICAE, the oil from the seeds OLEUM NUCISTAE, the red dried arillus MACIS, and the oil from the mace OLEUM MACIDIS.

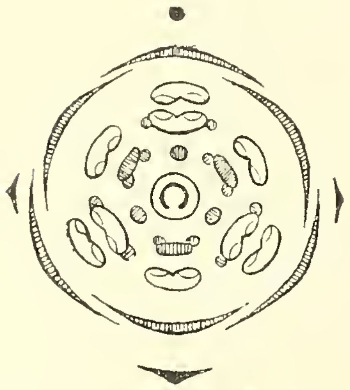


FIG. 510.—Floral diagram of *Persea.* (After EICHLER.)

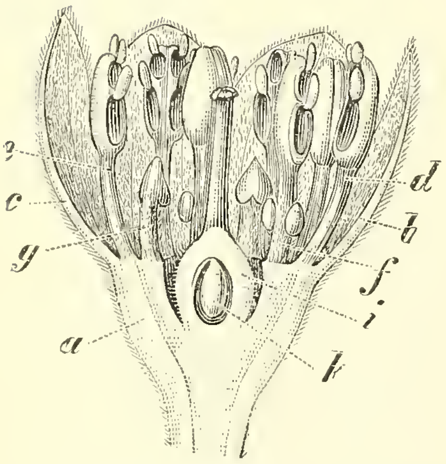


FIG. 511.—Flower of *Cinnamomum zeylanicum,* cut through longitudinally. *a,* Receptacle; *b,* outer, and *c,* inner leaves of perigone; *d-g,* stamens; *i,* pistil; *k,* ovule. (After BERG and SCHMIDT, magnified.)

FIG. 512.—*Cinnamomum zeylanicum.* *A,* Habit; *B,* vegetative bud. *OFFICINAL.* (After PAX, in *Nat. Pflanzenfamilien.*)

Family **Berberidaceae.**—Flowers trimerous; perianth of several whorls. *Berberis vulgaris.* OFFICINAL: PODOPHYLLINUM from the rhizome of *Podophyllum peltatum* (Fig. 508, North America).

Family **Menispermaceae.**—Tropical climbers related to the preceding. OFFICINAL: RADIX COLOMBO from *Jatrorrhiza palmata* (East Africa, Fig. 509).

Family **Lauraceae.**—Flowers PERIGYNOUS, CYCLIC, consisting throughout usually of trimerous whorls; perianth calycoid, small; stamens generally in FOUR WHORLS; ANTHERS WITH VALVES; gynœcium SYNCARPOUS; ovary unilocular, with a single suspended ovule; seeds without albumen. AROMATIC, woody plants (Figs. 510-514).

The majority of *Lauraceae* are trees with elliptical, entire leaves and small inconspicuous flowers aggregated in heads or panicles. The fruit is a berry or drupe, and is often surrounded at the base by the persistent receptacle. All parts of the plant contain, as a rule, ethereal oil accumulated in special cells.

FIG. 513.—*Cinnamomum camphora.*—*OFFICINAL.* (Reduced. After BERG and SCHMIDT.)

GEOGRAPHICAL DISTRIBUTION.—To the *Lauraceae* belong many of the most important trees of the warmer countries of both hemispheres; the order is almost wholly unrepresented in the Temperate Zone. Europe possesses but one species, *Laurus nobilis*, Sweet Bay (Mediterranean), a small evergreen tree with white

Fig. 514.—*Laurus nobilis.* Reduced. *Officinal.* (After Berg and Schmidt.)

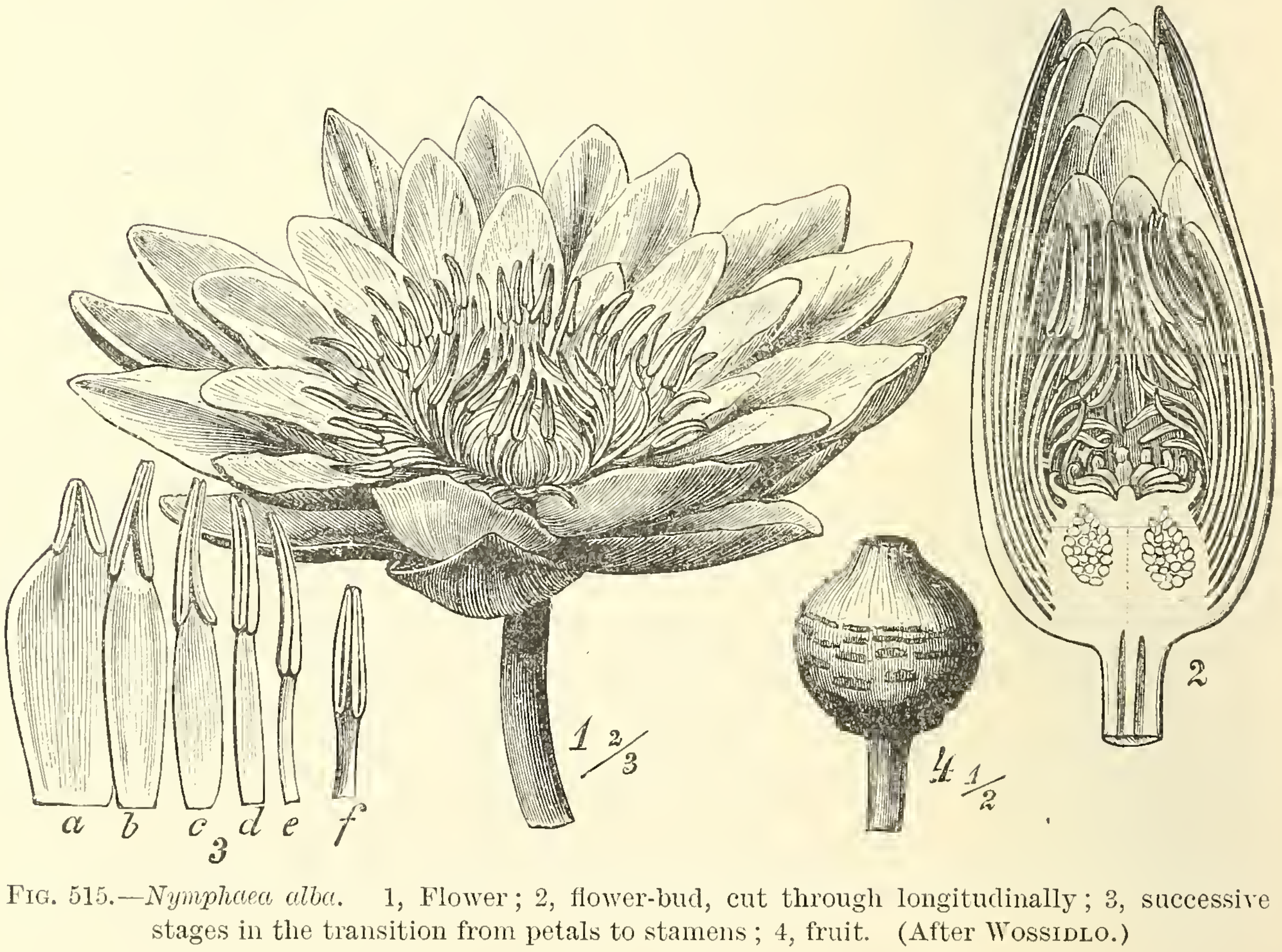


Fig. 515.—*Nymphaea alba.* 1, Flower; 2, flower-bud, cut through longitudinally; 3, successive stages in the transition from petals to stamens; 4, fruit. (After Wossidlo.)

flowers clustered in axillary, capitate inflorescences. The flowers, which are dimerous, and have bilocular anthers, produce a drupaceous fruit. The only herbaceous genus is *Cassytha*, a widely distributed tropical group of parasites, resembling the Dodder in appearance and habit.

OFFICINAL.—The fruit, FRUCTUS LAURI, of *Laurus nobilis* (Fig. 514); the bark and wood, SASSAFRAS, of *Sassafras officinale* (a diœcious, deciduous tree of North America); the gum, CAMPHORA, obtained from *Cinnamomum Camphora* (Fig. 513) (an evergreen tree, native of China and Japan); the bark, CORTEX CINNAMOMI, of *Cinnamomum Cassia* (a shrub of Southern China), and of the Cinnamon-tree, *Cinnamomum zeylanicum* (Figs. 511, 512) (Ceylon).

Family **Nymphaeaceae.**—Flowers hermaphrodite, hypogynous or epigynous, actinomorphic, with calyx and corolla, cyclic, or exclusive of the perianth, ACYCLIC; andrœcium and gynœcium usually POLYMEROUS; carpels apocarpous or syncarpous. WATER-PLANTS, USUALLY WITH LARGE FLOATING LEAVES (Figs. 515, 516).

In Europe, *Nymphaea* with inferior, *Nuphar* with superior ovary. In cultivation, *Victoria regia* (Equatorial South America), *Nelumbium speciosum*, Lotus of the Indians, *Nymphaea coerulea*, Lotus of the Egyptians.

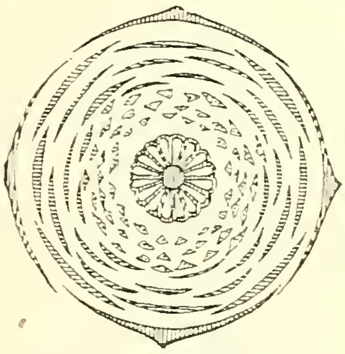


FIG. 516.—*Nymphaea*. Floral diagram.

Family **Ceratophyllaceae.**—Flowers small and greenish, with polymerous perigone, numerous stamens inserted upon a convex receptacle, and one carpel. Fruit a nut. A small family of submerged water-plants. One genus with three species.

Order 6. Rhoeadinae

Flowers hypogynous, hermaphrodite, predominantly DIMEROUS. Perianth consisting of three two- or four-merous whorls; andrœcium of two two-merous whorls; gynœcium dimerous, syncarpous; ovary UNILOCULAR, WITH PARIETAL PLACENTÆ. Herbs with alternate, simple leaves without stipules.

The *Rhoeadineae* constitute in themselves a natural, sharply defined order, and exhibit no marked affinity to other groups. The type of the order is best represented by the genus *Hypecoum*, in which the flowers are constructed throughout of simple dimerous whorls. In the largest families of the order, the *Cruciferae* and *Capparidaceae*, the corolla is tetramerous, alternating with the two decussate whorls of the calyx. It is often assumed, but without confirmatory evidence, that in such cases the four petals are derived by duplication from a dimerous corolla. The greatest variation is shown by the andrœcium, which, in consequence of the multiplication of its members, or more rarely of the whorls, frequently consists of more than four stamens. Even in such cases the derivation from the typical structure is generally recognisable. In the *Capparidaceae*, the successive processes in the evolution of the andrœcium are particularly apparent; in this family, all transitions occur from a 2 + 2-merous andrœcium to one that has become polymerous by repeated splitting; a reduction of the andrœcium to one whorl is also exhibited by some members of the family. The gynœcium usually remains dimerous; a multiplication of its carpels has taken place only in a few cases (*Papaver*).

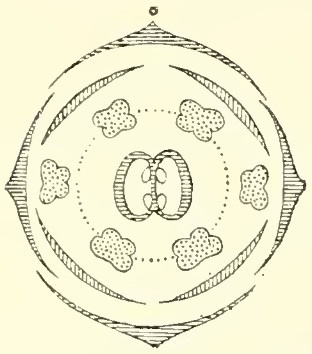


Fig. 517.—*Cruciferae.* Floral diagram (*Brassica*).

Family **Cruciferae**.—Flowers ACTINOMORPHIC; CALYX OF TWO TWO-MEROUS WHORLS; corolla TETRAMEROUS; andrœcium consisting of AN OUTER WHORL OF TWO SHORT STAMENS AND AN INNER OF FOUR LONG STAMENS DISPOSED IN PAIRS; gynœcium always dimerous; ovary DIVIDED BY FALSE DISSEPIMENTS INTO TWO LOCULI. Fruit rarely indehiscent, usually a capsule; SEEDS WITHOUT ENDOSPERM; embyro curved (Figs. 517-522).

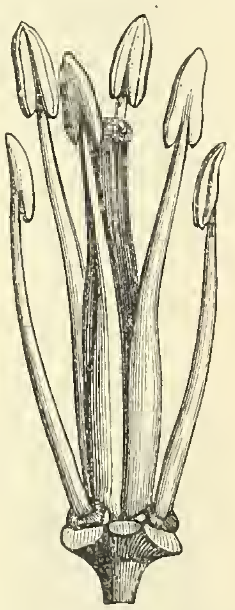


Fig. 518.—*Cardamine pratensis.* Flower with perianth removed. (After Baillon, × 4.)

The *Cruciferae* are glabrous or hispid herbs (rarely small shrubs) with entire, toothed or lobed leaves. The white or yellow flowers, rarely red or violet, are generally small and aggregated into racemes, usually without bracts and bracteoles. The flowers of the inflorescences develop so gradually in acropetal succession, that frequently the ripe fruit is already produced at the base of the raceme while the apex of the axis with its undeveloped buds is still in process of elongation (*e.g. Capsella bursa pastoris*). Although the colour of the petals, and also the nectaries at the base of the stamens, undoubtedly represent an attractive apparatus for insects, self-pollination is of frequent occurrence in this order. The capsules (Fig. 519) are either much longer than broad, and are then distinguished as SILIQUÆ, or they have the form of short and broad SILICULÆ. Indehiscent fruits occur less frequently. They are often lomentaceous in character and septated transversely by false partition-walls, breaking when ripe into a corresponding number of segments. A fruit of this nature is termed a JOINTED SILIQUA. The two forms of fruit, dehiscent and indehiscent, do not differ essentially in structure: both are sometimes borne by the same plant. Many *Cruciferae* contain a pungent, nitrogenous or sulphurous ethereal oil, which exists in an uncombined state in the vegetative organs (*e.g.* Horse-Radish), but in the seeds (*e.g.* Mustard seeds) it is combined, occurring in combination as a glucoside, from which it is freed by the presence of water or the action of an enzyme (*e.g.* Mustard seeds, cf. under Officinal).

The division of the *Cruciferae* into sub-families presents great difficulties. The old classification proposed by Linnæus is now regarded as too artificial. According to the nature of the fruit, Linnæus first distinguished the two groups *Siliquosae* and *Siliculosae*: these he further divided into *Siliquosae dehiscentes*, with normal siliquæ, *Siliquosae lomentaceae*, with jointed siliquæ, *Siliculosae* *dehiscentes*, with siliculæ, and *Siliculosae nucamentaceae*, with indehiscent fruits. The *Siliculosae dehiscentes* were afterwards divided by A. P. DE CANDOLLE into *S. latiseptae*, with broad, and *S. angustiseptae*, with narrow dissepiments.

Another classification frequently employed at the present time is that of DE CANDOLLE based on the position assumed by the embryo within the seeds—(1) *Notorrhizeae:* cotyledons flat, with the radicle lying on the surface of one of them; diagram, ○ || (Fig. 520, *B*). (2) *Orthoploceae:* cotyledons folded, the radicle lying in the groove of one of them; diagram, ○>> (Fig. 521). (3) *Pleurorrhizeae:* radicle lateral to the two cotyledons; diagram, ○= (Fig. 520, *A*). (4) *Spirolobeae:* cotyledons spirally rolled; diagram, ○ || ||. (5) *Diplecolobeae:* cotyledons doubly folded; diagram, ○ || || || ||. PRANTL has lately adopted a more natural classification, in which different organs (stigma, nectaries, dissepiments, hairs) are taken into consideration. The old classification of LINNÆUS and DE CANDOLLE has been used on account of its greater convenience.

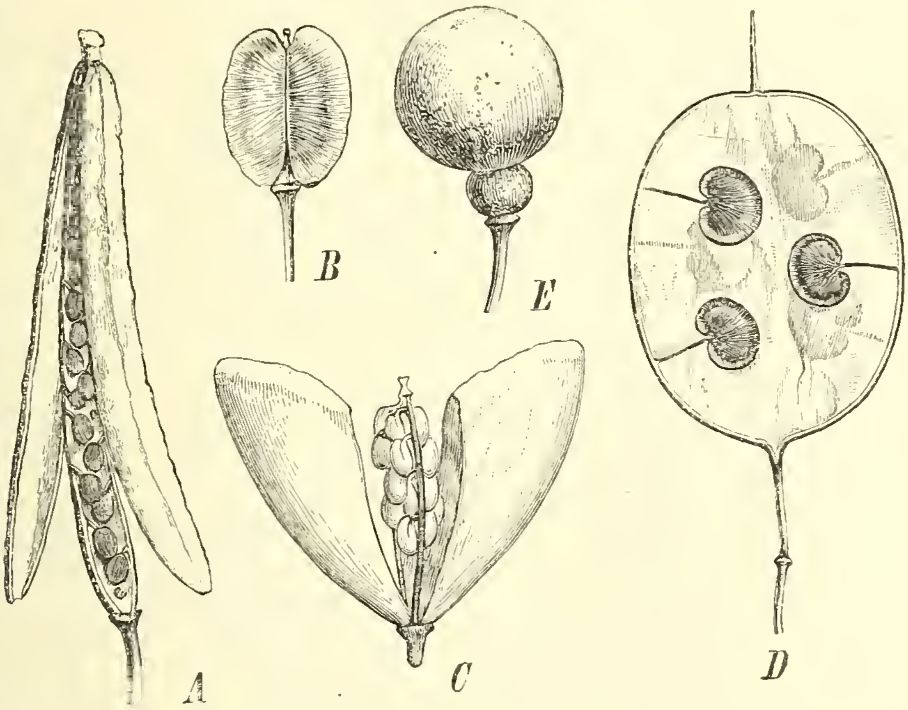


FIG. 519.—Cruciferous fruits. *A*, *Cheiranthus cheiri*; *B*, *Lepidium sativum*; *C*, *Capsella bursa pastoris*; *D*, *Lunaria biennis*, showing the septum after the carpels have fallen away. *E*, *Crambe maritima*. (After BAILLON.)

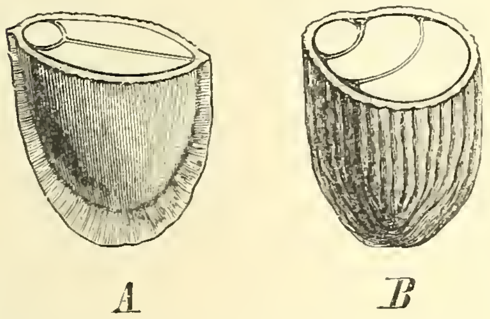


FIG. 520.—Seeds of *Cruciferae* cut across to show the radicle and cotyledons. *A*, *Cheiranthus cheiri* (× 8); *B*, *Sisymbrium alliaria* (× 7). (After BAILLON.)

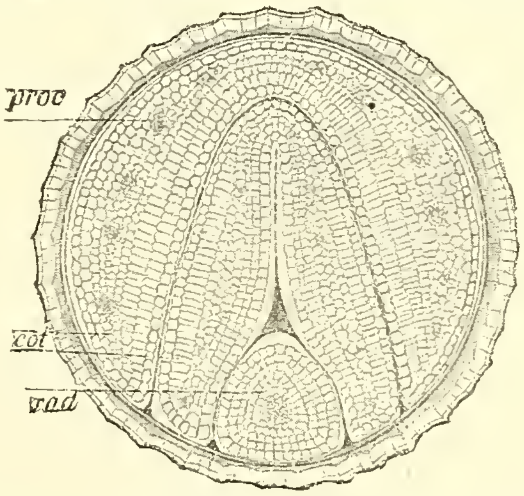


FIG. 521.—Transverse section of the seed of *Brassica nigra*. *rad*, radicle; *cot*, cotyledons; *proc*, vascular bundles. (After MÖLLER.)

REPRESENTATIVE GENERA. — (1) *Siliquosae dehiscentes:* *Cardamine* (Bitter

Cress), with elastic valves; *Arabis* (Rock Cress); *Barbarea* (Winter Cress); *Nasturtium*, in some cases with short siliquæ; *Cheiranthus* (Wall-flower); *Matthiola* (Stock); *Sisymbrium* (Hedge-Mustard); *Erysimum* (Treacle-Mustard); *Brassica; Sinapis* (Mustard). (2) *Siliquosae lomentaceae: Crambe* (Kale), *Cakile* (Sea Rocket), both strand plants; *Raphanus*, the siliqua of the Garden Radish, *R. sativus*, is spongy, not dividing into segments when ripe. (3) *Siliculosae dehiscentes latiseptae: Cochlearia; Draba* (Whitlow Grass), siliculæ lanceolate, somewhat compressed; *Alyssum; Lunaria* (Honesty), siliculæ very broad and flat, with long stalks; *Camelina* (False Flax). (4) *Siliculosae dehiscentes angustiseptae: Thlaspi* (Penny Cress), siliculæ flat, circular or cordate; *Iberis* (Candytuft), the racemes are corymbose, with marginal flowers slightly zygomorphic; *Capsella* (Shepherd's Purse), siliculæ triangular; *Lepidium* (Pepperwort). (5) *Siliculosae nucamentaceae: Isatis* (Woad).

FIG. 522.—*Cochlearia officinalis.* OFFICINAL. (After BAILLON.)

GEOGRAPHICAL DISTRIBUTION. — The *Cruciferae* are chiefly found in the North Temperate Zone, growing in the most varied situations. CULTIVATED SPECIES of this order are: *Brassica oleracea*, the Cabbage, in numerous varieties; the primitive form grows wild along the coast of Western Europe; *Brassica Napus* var. *oleifera*, Rape; var. *Napobrassica*, Turnip Cabbage; *Brassica Rapa*, Turnip; var. *oleifera*, Colza; *B. nigra*, Black Mustard; *Sinapis alba*, White Mustard; *Lepidium sativum*, Garden Cress; *Nasturtium officinale*, Water Cress; *Cochlearia Armoracia*, Horse-Radish; *Raphanus sativus*, Garden-Radish; *Camelina sativa*, Oil-seed or False Flax.

OFFICINAL.—*Brassica nigra*, the Black Mustard, yields SEMEN SINAPIS and OLEUM SINAPIS. *Sinapis alba*, the White Mustard, yields SEMEN ERUCAE. HERBA COCHLEARIAE is obtained from the herbaceous parts of *Cochlearia officinalis*, Scurvy Grass (Fig. 522), a glabrous herb growing wild on the sea-coast, bearing white flowers and globose siliculæ.

Family **Capparidaceae.**—Flowers usually ZYGOMORPHIC; OVARY STALKED. Herbs and shrubs of the warmer zones. The flower-buds of *Capparis spinosa*, a Mediterranean shrub, are familiar as CAPERS (Fig. 523).

Family **Fumariaceae.**—Flowers TRANSVERSELY ZYGOMORPHIC; calyx dimerous; corolla of TWO DIMEROUS WHORLS; andrœcium usually consisting of TWO TRIPARTITE STAMENS; gynœcium dimerous; SEEDS WITH ENDOSPERM (Fig. 524).

FIG. 523.—*Capparis spinosa.* 1, Flowering branch 2, fruit; 3, the same in transverse section. (After WOSSIDLO.)

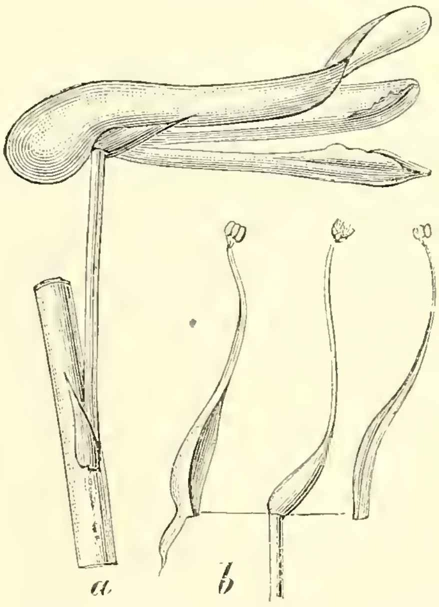


FIG. 524.—*Corydalis aurea.* *a*, Part of axis of raceme with a flower; *b*, style and stamens. (× 2.)

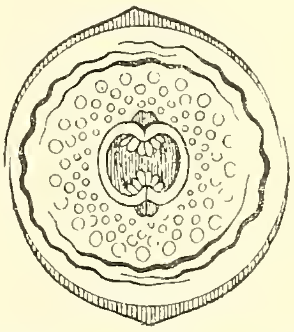


FIG. 525.—Floral diagram of *Glaucium.* (After EICHLER.)

The plants included in this family are glabrous, often glaucous herbs with divided leaves. The flowers are disposed in racemose inflorescences, with both subtending bracts and bracteoles, or in some cases with bracts only. One of the two outer petals and sometimes both are prolonged into a spur (*e.g.* *Fumaria*, *Corydalis*). The ANDRŒCIUM of *Hypecoum* consists of 2 + 2 stamens. The other genera have two tripartite stamens inserted opposite the outer petals; the central filament of each group bears a perfect anther, the two lateral filaments only half an anther each (Fig. 524, *b*). The modification from the normal type exhibited in such andrœcia is due to splitting and displacement of the stamens. The two lateral filaments, with their bilocular anthers, represent distinct halves of the inner stamens, that have become adherent to the stamens of the outer whorl.

The majority of this small family are natives of the North Temperate Zone. *Dicentra spectabilis*, with a two-spurred corolla, is a well-known ornamental plant.

Family **Papaveraceae.**—Flowers ACTINOMORPHIC; calyx dimerous; COROLLA CONSISTING OF TWO DIMEROUS WHORLS; andrœcium POLYMEROUS; pistil TWO- TO SIXTEEN-MEROUS; SEEDS WITH ENDOSPERM. Herbaceous plants with stiff hairs and LATEX VESSELS containing a white, more rarely a yellow, orange or red latex (Figs. 525, 526).

The flowers are usually large and beautifully coloured, either solitary or clustered. The fruit is always a many-seeded capsule, sometimes resembling the pods of the *Cruciferae*, but without false dissepiments.

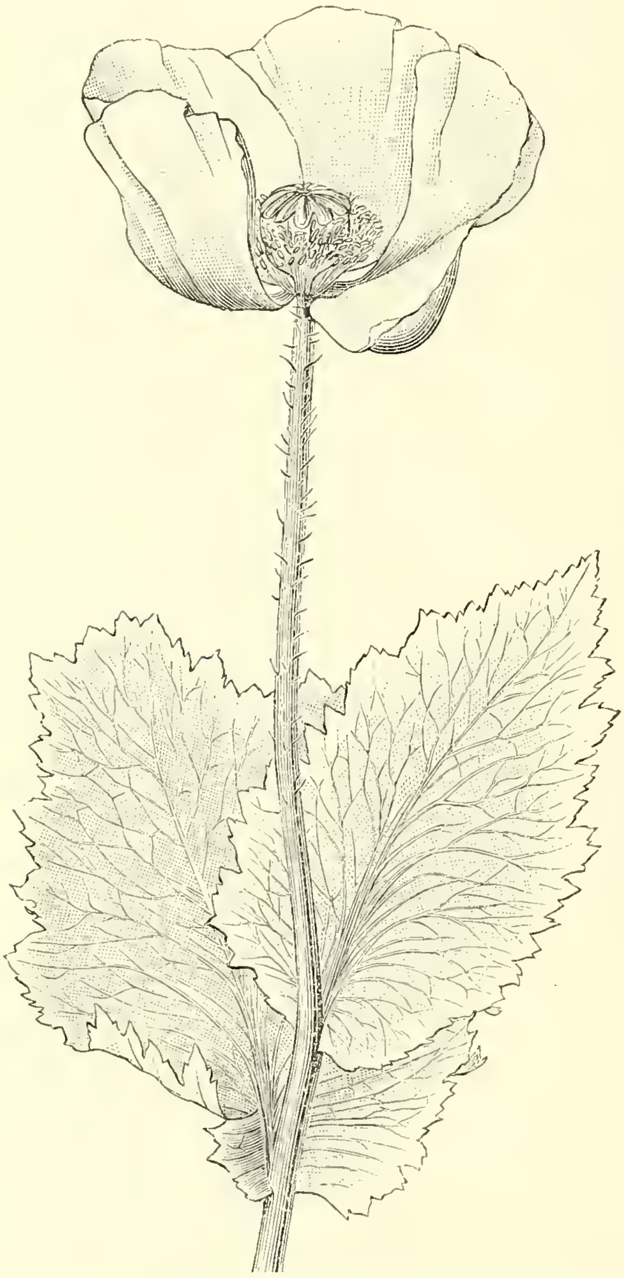


FIG. 526.—*Papaver somniferum* ($\frac{2}{3}$ nat. size). *POISONOUS* and *OFFICINAL*.

As examples of this family may be cited *Chelidonium* (Celandine), with orange-coloured latex and siliquose fruit; *Papaver* (Poppy), with white latex. In this last-named genus the fruit is an incompletely septated, polymerous capsule, opening at maturity by valves just below the rayed stigma.

GEOGRAPHICAL DISTRIBUTION.—The *Papaveraceae* constitute a small family restricted almost entirely to the North Temperate Zone.

POISONOUS.—*Papaver somniferum* (Opium Poppy) contains in all its organs a poisonous, milky latex. It is an annual herb with glabrous, somewhat glaucous stems and leaves, and is cultivated for the sake of the oil accumulated in the seeds, also for the latex obtained from the unripe capsules; the latex, on hardening, constitutes opium. The leaves are sessile, irregularly incised and toothed. The flowers are solitary, borne upon a long stalk with bristly hairs (Fig. 526). They are nodding while in the bud, but become afterwards erect; they have a fugacious calyx and white or violet petals with crumpled æstivation. The fruit is a broad capsule more than 6 cm. in length, enclosing numerous reniform seeds of a white or violet colour. Other species of *Papaveraceae* are also toxic, but in a less degree.

OFFICINAL.—*Papaver somniferum*, yielding FRUCTUS PAPAVERIS IMMATURI, Semen Papaveris, Oleum Papaveris, Opium, and Morphinum. *Papaver Rhoeas* yields Flos Rhoeados.

Family **Resedaceae.**—Flowers ZYGOMORPHIC, perianth consisting of two- to eight-merous whorls; petals deeply fringed. Sexual organs usually BORNE UPON A GYNOPHORE; stamens three to forty; carpels two to six, FREE OR UNITED, forming a unilocular OVARY OPEN AT THE APEX. *Reseda luteola* (Dyer's Weed), *R. lutea* (Base Rocket), *R. odorata* (Mignonette).

There is considerable uncertainty as regards the systematic position of the plants included in the family *Resedaceae;* they are considered to be allied to the *Capparidaceae.*

Order 7. Cistiflorae

Flowers hypogynous, generally actinomorphic and hermaphrodite. Calyx imbricated in the bud; the whorl of the perianth and andrœcium typically pentamerous, but the andrœcium often POLYMEROUS by the division of the stamens; gynœcium usually three- to five-merous, and syncarpous; OVARY UNILOCULAR, with parietal placentæ, less frequently multilocular; ovules for the most part anatropous; embryo usually straight; leaves simple, usually alternate.

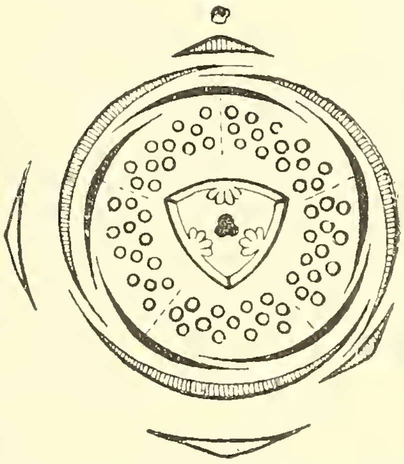


FIG. 527.—Floral diagram of *Helianthemum vulgare.* (*Cistaceae.*) (After EICHLER.)

The *Cistiflorae* form a somewhat artificial order; they comprise families which, in most cases, have been previously assigned to different systematic positions. The flowers exhibit the regular Dicotyledonous type or a modification of it, resulting from the division or suppression of some of their parts, but without at the same time showing any uniformly occurring characteristics of general significance. There is, moreover, in this order no predominant type about which the less distinctive forms may be grouped. Many of the *Cistiflorae* show an affinity to the *Resedaceae,* and through them to the *Rhoeadinae;* others, in particular the *Ternstroemiaceae,* to the *Columniferae;* and some are allied to the *Passiflorinae.*

Family **Cistaceae.**—Flowers actinomorphic, with NUMEROUS STAMENS; gynœcium three- to five-merous; ovary usually unilocular, with parietal placentæ; STYLE SIMPLE; OVULE ATROPOUS; fruit a capsule; seeds with endosperm; embryo curved; small woody plants; more rarely herbs, with simple leaves (Figs. 527, 528), *Helianthemum.*

Family **Violaceae** (32).—Flowers actinomorphic, or more FREQUENTLY ZYGOMORPHIC; stamens five; ovary unilocular, with parietal placentæ, STYLE SIMPLE; seeds albuminous, with straight embryo (Figs. 529, 530).

The family includes herbs, shrubs, and trees, frequently with leaves having large stipules; it is represented, though not by a large number of genera, in all zones. *Viola,* the Violet, Pansy or Heart's-ease, has always axillary, zygomorphic flowers with the anterior petal prolonged into a hollow spur enclosing spur-like nectarial appendages of the two lower stamens (Fig. 530, *B*, *nt*). Many species of *Viola*, in addition to the conspicuous flowers provided with nectaries and adapted to insect-pollination, bear cleistogamous flowers which contain no honey and are self-pollinated (cf. p. 284). The entomophilous flowers, although so well equipped, are very often sterile. Many forms are in cultivation derived by crossing from several species (*V. altaica*, *V. tricolor*, *V. lutea*, etc.).

FIG. 528.—*Helianthemum vulgare* (nat. size). (After WOSSIDLO.)

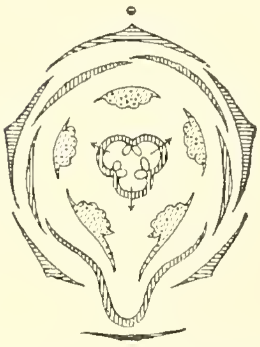


FIG. 529.—Floral diagram of *Viola*.

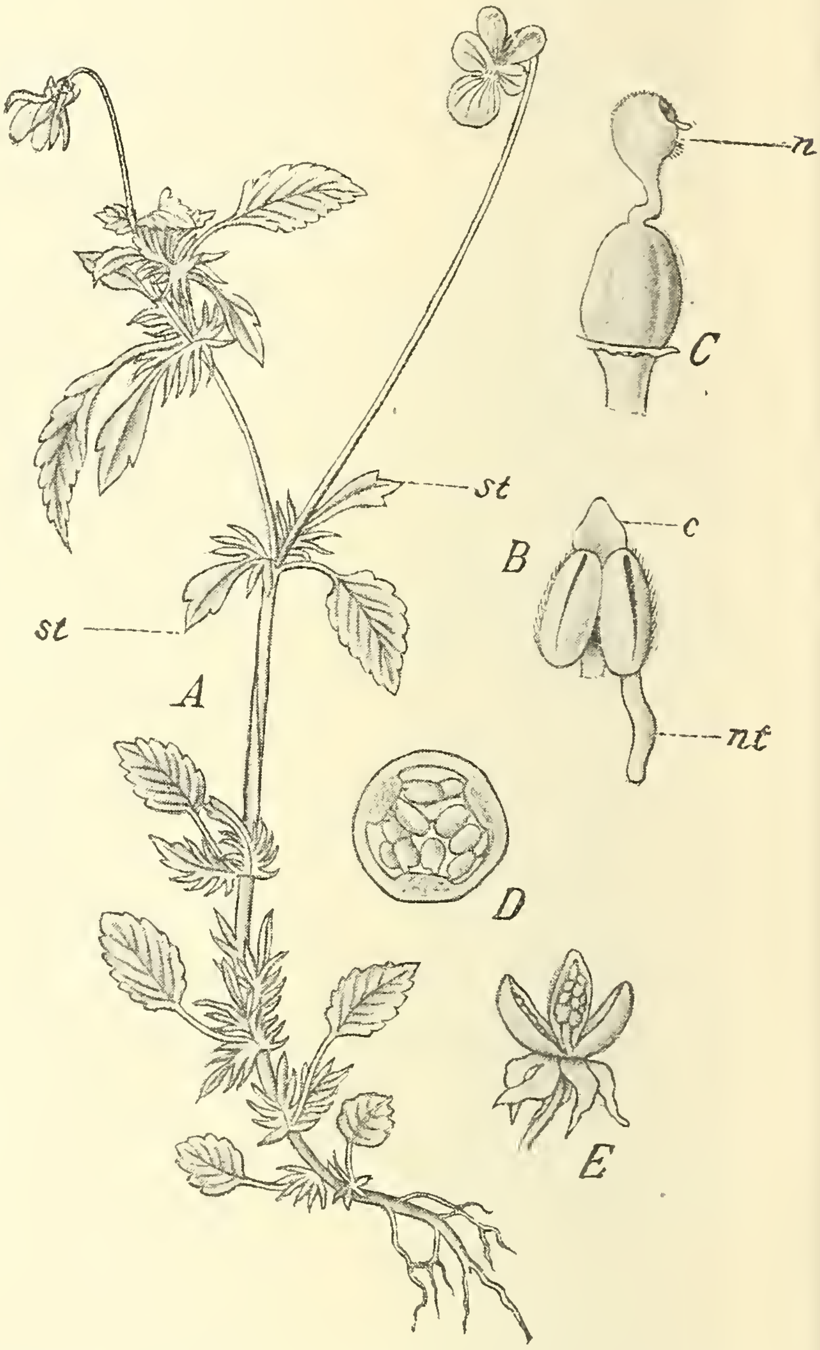


FIG. 530.—*Viola tricolor*. *A*, Entire plant (reduced); *B*, a stamen, enlarged; *C*, gynœcium, enlarged; *D*, transverse section of ovary; *E*, fruit (nat. size).—*OFFICINAL*.

OFFICINAL.—HERBA VIOLAE TRICOLORIS is obtained from *Viola tricolor*.

Family **Hypericaceae**.—Flowers actinomorphic, stamens three or five, DEEPLY DIVIDED INTO NUMEROUS BRANCHES; ovary unilocular or multilocular, with parietal placentæ and free styles; seeds WITHOUT ENDOSPERM. LEAVES OPPOSITE, DOTTED WITH OIL-GLANDS (Fig. 531).

Members of this family are found widely distributed in both the temperate and warmer zones. Many species of *Hypericum* (*e.g.* the common St. John's-wort, *H. perforatum*) are common wayside weeds.

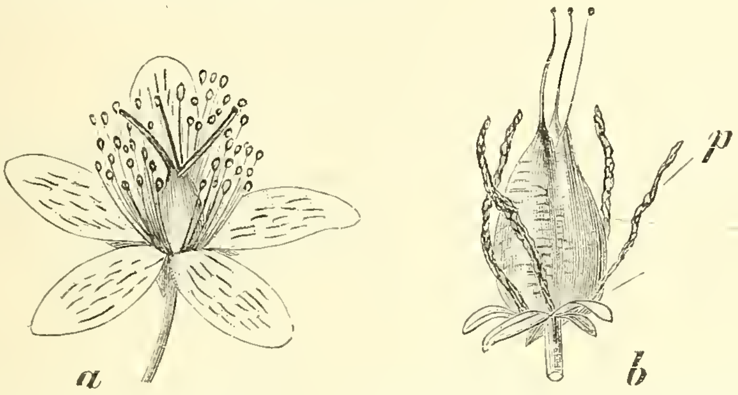


Fig. 531.—*Hypericum tetrapterum.* *a*, Flower, somewhat magnified ; *b*, fruit ; *p*, the dried, persistent petals. (× 2.)

Family **Droseraceae.**—Insectivorous plants (cf. p. 214, Fig. 189). *Drosera* on moors.

Family **Clusiaceae.**—Tropical trees with gum-resin canals.

Officinal.—The dried gum-resin from *Garcinia hanburyi* (East Indies).

Fig. 532.—*Thea chinensis.* 1, Flowering branch ; 2, flower cut through longitudinally ; 3, fruit ; 4, seed. (After Wossidlo.)

Family **Ternstroemiaceae.**—Evergreen woody plants, *Camellia japonica.*

Officinal.—*Thea chinensis* (Fig. 532), a shrub cultivated in China and the East Indies, yields tea, Folia Theae.

Family **Tamaricaceae.**—*Myricaria, Tamarix.*

Family **Dipterocarpaceae.**—Officinal.—*Shorea Wiesneri,* an East Indian tree, provides Resina Dammar.

Order 8. Passiflorinae

Flowers actinomorphic, mostly PERIGYNOUS or EPIGYNOUS; gynœcium TRIMEROUS; ovary UNILOCULAR, with PARIETAL PLACENTÆ.

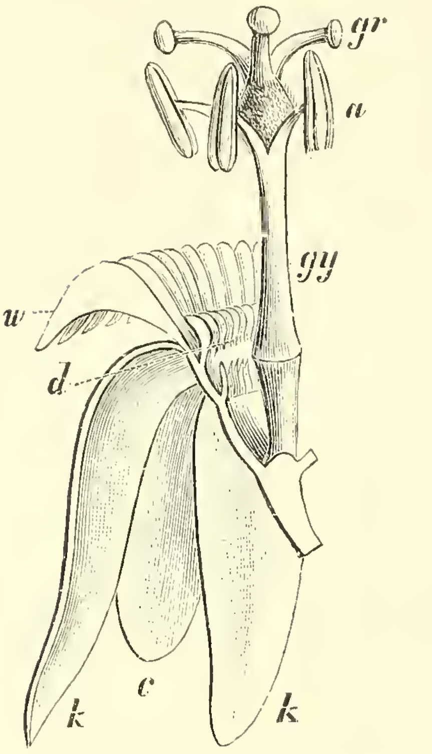


FIG. 533.—*Passiflora Engleriana*. Part of a flower. *k*, Sepals; *c*, a petal; *w*, corona; *d*, disc; *gy*, gynophore; *a*, anthers; *gr*, stigmas, nat. size. (After HARMS in *Natürl. Pflanzenfamilien*.)

Family **Passifloraceae.**—Climbing plants with large flowers; the flowers are complicated in structure owing to outgrowths of the axis (corona, disc) (Fig. 533), *Passiflora*, Passion flower from South America.

Family **Caricaceae.**—*Carica papaya* (Papaw) contains a peptonising ferment (papayotin) in its latex.

Family **Begoniaceae.**—Herbs with oblique, heart-shaped leaves. Flowers unisexual. Ovary inferior. Tropical. Many species of *Begonia* are cultivated.

Order 9. Opuntinae

With the single family **Cactaceae** (33).—Flowers epigynous, actinomorphic, hermaphrodite; perianth and androecium ACYCLIC; gynœcium consisting of a LARGE, INDEFINITE NUMBER OF CARPELS; ovary UNILOCULAR, with many PARIETAL PLACENTÆ; ovules with long funiculi; fruit a berry. Herbaceous and woody plants, with fleshy axes and usually REDUCED, THORN-LIKE LEAVES (Figs. 28, 534).

In many *Cactaceae* (*e.g. Mamillaria*) the assimilatory vegetative system is reduced to an angular, cylindrical, or spherical axis, entirely destitute of foliage-leaves; in other *Cactaceae*, again, the assimilatory organs are represented by a system of branching axes which may be prismatic (*Cereus*) or flattened, either band-shaped (*Epiphyllum*, Fig. 534) or ovate (*Opuntia*, Fig. 28). The clusters of spines occurring on the axes represent in most cases reduced leaves. *Peireskia* is the only genus possessing well-developed foliage-leaves.

FIG. 534.—*Epiphyllum truncatum*. 2, Flower cut through longitudinally. (Nat. size, after WOSSIDLO.)

Peculiar as the general appearance of the *Cactaceae* is, it is not distinctively characteristic of this family alone, as some of the *Euphorbiaceae* and *Asclepiadaceae* possess a similar habit.

GEOGRAPHICAL DISTRIBUTION.—The large family of the *Cactaceae* is restricted to the warmer countries of America. Like most succulents, the plants of this group are typically xerophilous, although they occasionally occur as epiphytes on the dry bark of trees in damp forests. They attain their greatest development in the dry regions in the south-western part of North America, where the columns of the Monument Cactus, *Cereus giganteus*, with their candelabra-like branches, tower 20 m. high above the naked, rocky soil. They are especially prevalent in the high table-lands of Mexico, and, extending almost to the snow-line, exhibit the most astonishing diversity of form. One species, *Opuntia ficus indica*, with edible berries, has escaped from cultivation in the neighbourhood of the Mediterranean, and, like the American *Agave*, has become so common that it is now a characteristic plant of that region. It is on this plant that the Cochineal insect is cultivated. The *Cactaceae* are largely cultivated as hot-house and window plants.

Order 10. Columniferae

Flowers hypogynous, hermaphrodite, actinomorphic, with valvate calyx and pentamerous perianth; stamens usually MONADELPHOUS, although typically five in number, becoming INDEFINITE by division; carpels 2 – ∞; ovary syncarpous, SEPTATE, corresponding to the number of carpels.

The andrœcium, in particular, is characteristic of the *Columniferae*. In some forms it is constructed, according to the Dicotyledonous type, of two pentamerous whorls; but in the majority of cases one whorl, usually the episepalous, is suppressed or replaced by staminodia, while the other, in consequence of the division of the staminal rudiments, consists of a larger number of members. In addition, the filaments of the stamens in most *Columniferae* are united into a longer or shorter column, or, more appropriately described, into a tube, whose derivation from the five or ten original rudiments is only recognisable after investigation of its mode of development and a comparison with allied forms. A division of the carpels, similar to that of the stamens, is also of frequent occurrence in the gynœcium.

Family **Tiliaceae.**—SEPALS FREE; PETALS VALVATE in the bud; stamens usually numerous, FREE; anthers INTRORSE, dithecious; pollen-grains NOT SPINY (Figs. 535, 536).

The *Tiliaceae* are for the most part woody plants, with toothed or lobed stipulate leaves. The flowers, which are adapted to insect-pollination, are united in clusters, and produce a dry capsule or an indehiscent fruit.

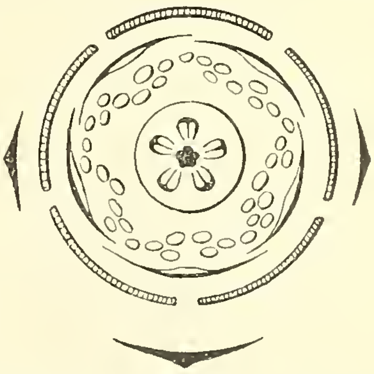


FIG. 535.—*Tiliaceae.* Floral diagram (*Tilia*). (After EICHLER.)

The andrœcium consists in some species of two pentamerous whorls, thus representing the primitive type from which the more complicated andrœcia of other forms have developed. Sometimes by the suppression of one whorl, either the epipetalous or the episepalous, the number of stamens is reduced to five, or, in other instances, one whorl is represented by staminodia. In most cases, however, the number of stamens is indefinite in consequence of a division of the staminal rudiments extending to their very base, the stamens being grouped correspondingly in either five or ten bundles. In some forms they are united at the base, just as in the *Malvaceae*, but the andrœcia of the *Tiliaceae* are always distinguishable by their dithecious, introrse anthers and smoother pollen-grains. The stamens in some species, again, are in part transformed into petaloid staminodia (*e.g. Tilia tomentosa*).

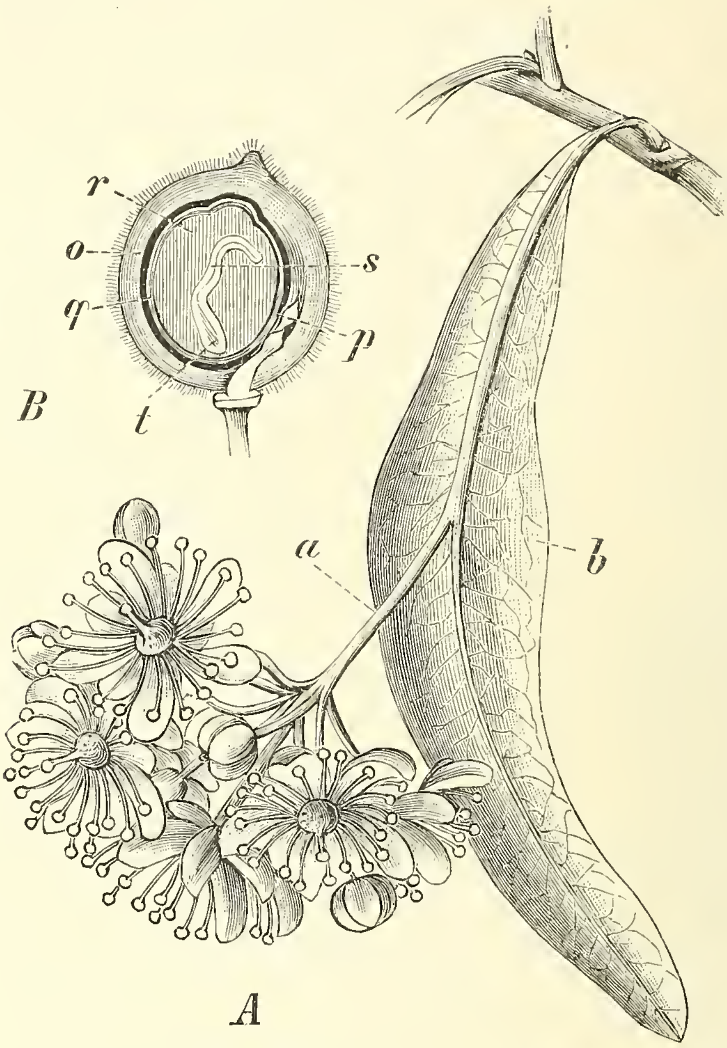


FIG. 536.—*Tilia ulmifolia.* *A*, Inflorescence (*a*), with hypsophyll *b* (nat. size). *B*, Longitudinal section of fruit (magnified); *o*, pericarp; *p*, atrophied dissepiment and ovule; *q*, seed; *r*, endosperm; *s*, embryo; *t*, its radicle.—OFFICINAL. (After BERG and SCHMIDT.)

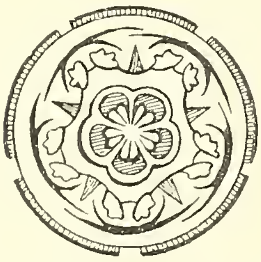


FIG. 537.—*Sterculiaceae.* Floral diagram (*Theobroma*). (After EICHLER.)

This family, which is chiefly tropical, is represented in northern regions only by the genus *Tilia*, variously known under the name of Linden, Basswood, or Lime-tree. Lime-trees have two-ranked leaves with small stipules, and flowers aggregated in a cymose umbel. The slender stalk of each inflorescence is adnate to an elongated hypsophyll, differing from the foliage-leaves (Fig. 536) both in its yellowish colour and shape. The numerous stamens are developed from five episepalous rudiments, and in older flowers are distinctly grouped in five bundles. The ovary is hairy, contains two ovules in each of the five loculi, and ripens into an indehiscent fruit with a single endospermous seed. *Tilia ulmifolia* (=*parvifolia*) has five- to nine-flowered inflorescences and heart-shaped leaves, which are beset on the under side, in the angles of the nerves, with brown tufts of hair, but otherwise are glabrous; the large-leafed

Linden, *T. platyphyllus* (= *T. grandifolia*), has leaves, hairy on the under surface, and three- to five-flowered inflorescences. The flowers of *T. tomentosa* have five white staminodia resembling the petals.

Officinal.—Both *Tilia ulmifolia* and *platyphyllus*, yielding Flores Tiliae.

Family **Sterculiaceae.**—Flowers often apetalous; calyx GAMOSEPALOUS; petals CONTORTED; stamens usually NOT VERY NUMEROUS, monadelphous; anthers EXTRORSE, DITHECIOUS; pollen-grains not often spiny (Figs. 537-540).

FIG. 538.—*Theobroma Cacao.* Branch with flowers.—*Officinal.* $\frac{2}{3}$ nat. size. (After Berg and Schmidt.)

The andrœcium of this family, unlike that of the *Tiliaceae*, is always monadelphous. It resembles in this respect the andrœcium of the *Malvaceae*, from which, although sometimes only distinguishable by the dithecious anthers, it differs in having, as a rule, a much smaller number of stamens. The episepalous stamens are never fertile, but are either staminodial or suppressed.

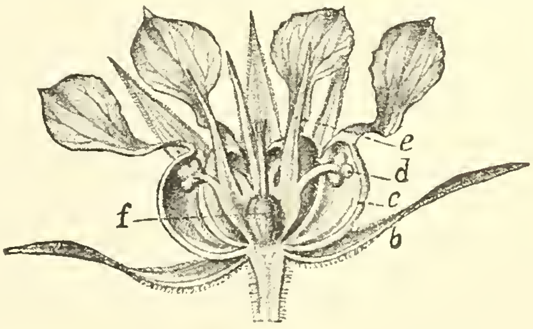


FIG. 539.—*Theobroma Cacao.* Flower in median section. Magnified. (After Berg and Schmidt.)

The *Sterculiaceae* are almost exclusively confined to the Tropics, where they are constantly met with either as herbaceous plants, shrubs, lianes, or trees, often bearing flowers of a peculiar and unusual form. The only plant in this group of value to man is the Cacao-tree, *Theobroma Cacao*, a small tree, originally native of Mexico, but now cultivated in all tropical countries. The small flowers are red in colour, and spring from the cortex of the stem and older branches. The fruit, which is about the size of a small cucumber, and of red or orange colour, has a hard longitudinally-ribbed wall, and contains numerous disc-shaped seeds embedded within its juicy flesh. After fermentation, when roasted and ground, chocolate and cacao are obtained from the seeds.

OFFICINAL.—The seeds of *Theobroma Cacao*, yielding Cocoa-butter, OLEUM CACAO. Kola nuts, SEMEN COLAE, which have recently been recommended for their medicinal qualities, are derived from *Kola vera* and *acuminata* (West Africa).

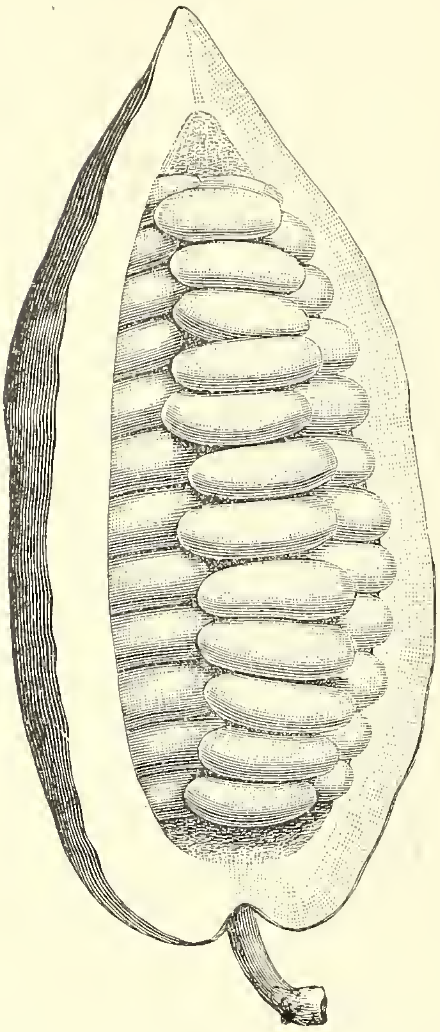


FIG. 540.—Fruit of *Theobroma Cacao*, with a portion of the pericarp removed ($\frac{1}{2}$ nat. size). —*OFFICINAL*. (After BERG and SCHMIDT.)

Family **Malvaceae**.—Calyx GAMOSEPALOUS; PETALS CONTORTED IN THE BUD; stamens NUMEROUS, MONADELPHOUS; anthers EXTRORSE, MONOTHECIOUS; pollen-grains SPINY (Figs. 541-544).

The *Malvaceae* are herbaceous or woody plants, abounding in mucilage, and usually, at least in their early growth, covered with matted woolly hair. The leaves are palmately nerved and frequently palmately lobed. The funnel or bell-shaped flowers are entomophilous, generally large and beautifully coloured. They are either solitary and axillary, or grouped in terminal inflorescences, and are often provided with an involucre or epicalyx, formed of three or more bracteoles. The petals are slightly united at the base. The numerous monothecious stamens are formed as the result of a splitting of the epipetalous whorl, which in this case extends to the anthers, while the episepalous whorl is either entirely suppressed or represented by tooth-like staminodia attached to the top of the staminal tube. The gynœcium is often multicarpellary, and gives rise to a capsule or schizocarp.

REPRESENTATIVE SUB-FAMILIES.—(1) *Malveae*, with schizocarpous fruit, produced from numerous carpels arranged in a whorl; *e.g. Malva*, with epicalyx consisting of three free involucral bracteoles; *Lavatera*, with epicalyx of three united bracteoles; *Althaea*, with epicalyx of six to nine bracteoles united at the base. (2) *Hibisceae*, with fruit in the form of a capsule; *e.g. Hibiscus* (Rose-Mallow), *Gossypium* (the Cotton-plant).

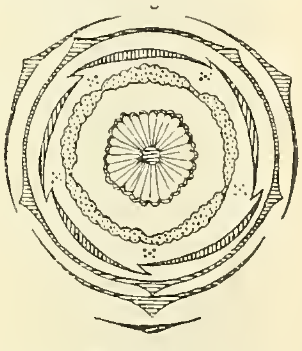


FIG. 541.—*Malvaceae*. Floral diagram (*Malva*).

GEOGRAPHICAL DISTRIBUTION.—With the exception of the polar regions, members of the Mallow family are found distributed over the whole earth, although chiefly occurring in the warmer zones. *Althaea rosea*, the Hollyhoek, and some of the bushy species of *Hibiscus* are favourite ornamental plants. The species of *Gossypium*, from which cotton is obtained, are mostly shrubs with lobed leaves and bell-shaped yellow or red flowers. The Cotton-plant, which still grows wild in tropical countries, is largely cultivated in all the warmer regions of Asia and America. The fruit (Fig. 544) is a capsule packed with white, yellow, or brown hairs (cotton), which are attached to the seeds (3), and serve as an aid to wind-distribution.

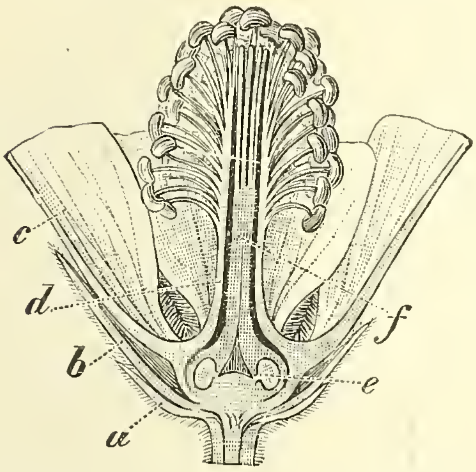


FIG. 542.—Flower of *Althaea officinalis*, cut through longitudinally. *a*, Outer; *b*, inner calyx; *c*, petals; *d*, androecium; *f*, pistil; *e*, ovule (magnified). (After BERG and SCHMIDT.)

FIG. 543.—*Malva silvestris*. *a*, Flower; *b*, flower-bud; *c*, fruit (nat. size.)—*OFFICINAL*.

FIG. 544.—*Gossypium herbaceum*. 1, Flowering branch; 2, fruit; 3, seed (nat. size). *OFFICINAL*. (After WOSSIDLO.)

OFFICINAL.—*Malva neglecta* and *M. silvestris* (High-Mallow) supply FOLIA

Malvae, and *M. silvestris* (Fig. 543) also Flores Malvae. The leaves, Folia Althaeae, and the roots, Radix Althaeae, of *Althaea officinalis* (common Marsh-Mallow) are used medicinally. Cotton-wool is obtained from *Gossypium*.

Order 11. Gruinales

Flowers hypogynous, hermaphrodite, actinomorphic, and pentamerous throughout, or zygomorphic, and then often reduced, NEVER WITH POLYMEROUS WHORLS FORMED BY SPLITTING; stamens MONADELPHOUS AT THE BASE, obdiplostemonous; DISC ABSENT; ovary syncarpous, SEPTATED; micropyle DIRECTED UPWARDS.

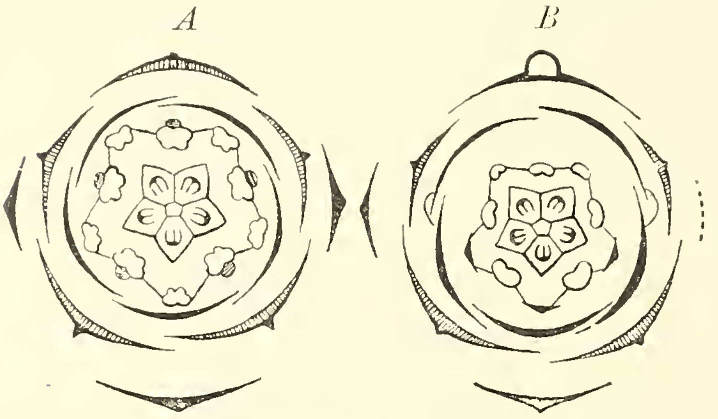


Fig. 545.—Floral diagrams of *Geraniaceae*. *A*, *Geranium pratense*; *B*, *Pelargonium zonale*. (After Eichler.)

The *Gruinales* are distinguished from the *Columniferae* by the partially monadelphous stamens, and by the absence of splitting in the androecium. In both orders one whorl of stamens is often suppressed or replaced by staminodia. The absence of a disc and the position of the micropyle distinguish the *Gruinales* from the allied order *Terebinthinae* and the *Aesculinae*.

Family **Geraniaceae.**—Flowers actinomorphic, rarely zygomorphic, pentamerous throughout; stamens five or ten; ovary with TWO ovules in each loculus; carpels prolonged into an AWN, and BECOMING DETACHED, WHEN RIPE, FROM A PERSISTENT CENTRAL COLUMN (Figs. 545, 546).

The *Geraniaceae* are herbs, or, in warm climates, small shrubs, with simple leaves and usually with glandular hairs, which secrete an aromatic oil. The flowers are either axillary and solitary or clustered in inflorescences of various types, and have usually a carmine or crimson corolla. The carpels in many species remain closed, and are forced into the ground by the movements of the spirally-twisting hygroscopic awn (*e.g. Erodium*). In most of the large-flowered species of *Geranium* the awns, in coiling, contract with such suddenness that the seeds are shot out from the carpels, which rupture along the ventral suture. The two genera may readily be distin-

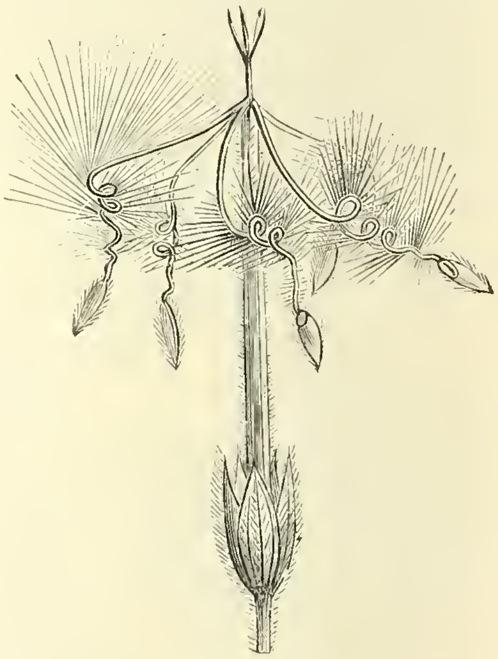


Fig. 546.—Fruit of *Pelargonium inquinans*, × 3. (After Baillon.)

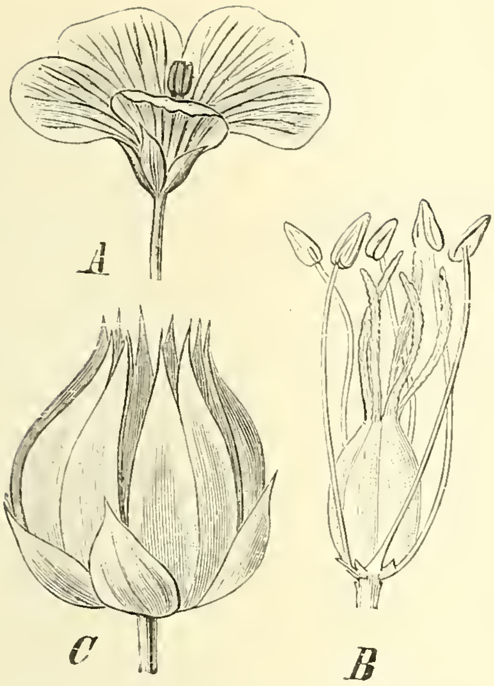


Fig. 547.—*Linum usitatissimum.* *A*, Flower; *B*, andrœcium and gynœcium; *C*, capsule after dehiscence (*A*, nat. size; *B*, *C*, × 3).—*Officinal.*

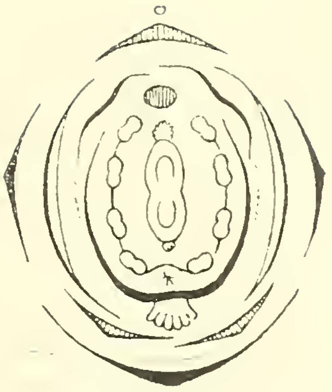


Fig. 549.—Floral diagram of *Polygala Myrtifolia.* (After Eichler.)

Fig. 548.—*Erythroxylum Coca.*—*Officinal.* (After Schumann and Arth. Meyer.)

Fig. 550.—*Polygala Senega* (½ nat. size). — *Officinal.* (After Berg and Schmidt.)

guished, as *Erodium* (Storksbill) has only five stamens, while in *Geranium* (Cranesbill) ten are present.

Geographical Distribution.—Members of this family are found widely scattered over all zones. The various species of *Pelargonium* (flowers zygomorphic), which are so largely cultivated, are indigenous to South Africa.

Family **Tropaeolaceae.**—*Tropaeolum majus*, Indian cress, and other species in cultivation.

Family **Oxalidaceae.**—Leaves compound. *Oxalis Acetosella*, wood sorrel, contains oxalic acid.

Family **Linaceae.**—Flowers ACTINOMORPHIC; four- or five-merous; stamens monadelphous, the epipetalous whorl WANTING OR STAMINODIAL; each loculus of the ovary incompletely halved by a FALSE DISSEPIMENT, and having one ovule in each chamber; fruit drupaceous or else a capsule. Herbs and shrubs with NARROW, ENTIRE LEAVES (Fig. 547).

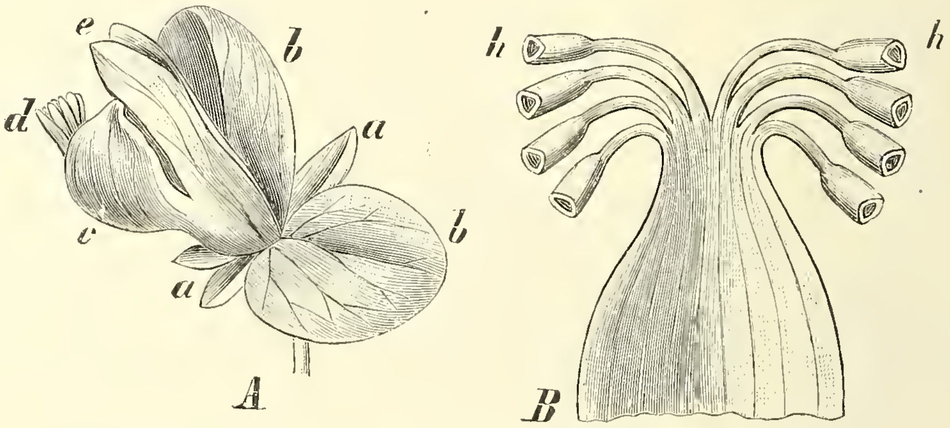


Fig. 551.—*Polygala Senega.* *A*, Flower; *a*, small, *b*, large sepals; *c*, keel; *e*, lateral petals; *d*, andrœcium. *B*, andrœcium; *h*, anthers (magnified).—*Officinal.* (After Berg and Schmidt.)

The only plant of economic value in this family is the Flax, *Linum usitatissimum*, an annual herb, native of Western Asia, and known in cultivation since the earliest historic ages. The flowers (Fig. 547) are blue, and borne in cymose inflorescences. Linen is woven from the strong bast-fibres of the stems, while the seeds are also of value on account of the oil (linseed oil) extracted from them.

Officinal.—*Linum usitatissimum* yields Semen Lini and Oleum Lini.

Family **Balsaminaceae.**—Flowers ZYGOMORPHIC, with five FREE stamens; fruit a capsule, BURSTING WHEN RIPE INTO VALVES. Herbs with simple leaves.

Impatiens noli tangere in woods. *I. parviflora* and *I. Balsamina* are cultivated ornamental plants.

Family **Erythroxylaceae.**—

Officinal.—*Erythroxylum Coca* (Fig. 548), a shrub growing in Bolivia and Peru. Its leaves (Folia Coca) contain the alkaloid Cocaine.

Family **Polygalaceae.**—Flowers ZYGOMORPHIC, WITH INCOMPLETE WHORLS, the corolla being reduced to three petals, and the andrœcium to eight stamens UNITED INTO A TUBE; gynœcium DIMEROUS; fruit a capsule or drupe (Figs. 549-551).

The *Polygalaceae* include herbs, shrubs, and lianes, with simple leaves: they are widely distributed over the whole globe. Their flowers in general appearance somewhat resemble those of the *Papilionaceae*, but the wings belong to the calyx and not to the corona. The keel, however, is a petal. The anthers open by pores. The various species of Milkwort (*Polygala*) are familiar representatives of this family.

OFFICINAL.—The North American Senega, Snakeroot (*Polygala Senega*), supplies the officinal RADIX SENEGA.

Order 12. Terebinthinae

Flowers as in the preceding order, but with AN INTRA-STAMINAL

FIG. 552.—*Pilocarpus pennatifolius* (½ nat. size).—*OFFICINAL.* (After SCHUMANN and A. MEYER.)

DISC. For the most part woody plants, with ETHEREAL OILS which occur in canals or cells.

This order stands in close relation with the *Gruinales*, with which it is now sometimes united. The fact, however, that in the majority of cases members of this order exhibit special characteristics which, although sometimes modified, are traceable throughout the varying forms of the order, would seem to indicate their common origin. Thus the majority of the *Terebinthinae* are aromatic woody plants, with pinnate, persistent glabrous leaves and small or at most medium-sized flowers, which possess a fleshy disc at the base of the ovary, and are disposed in racemose or cymose inflorescences. They are found chiefly in warm countries, growing in dry and sunny situations.

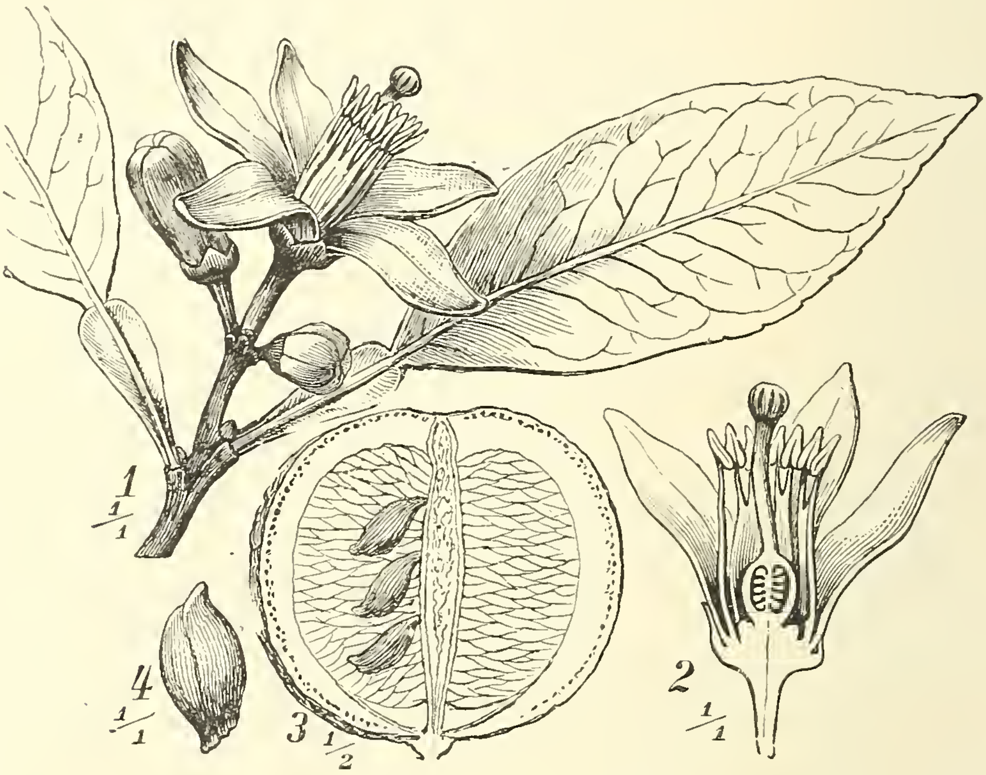


Fig. 553.—*Citrus Aurantium.* 1, Flowering branch ; 2, a flower cut through longitudinally ; 3, fruit in longitudinal section ; 4, seed.—*OFFICINAL.* (After WOSSIDLO.)

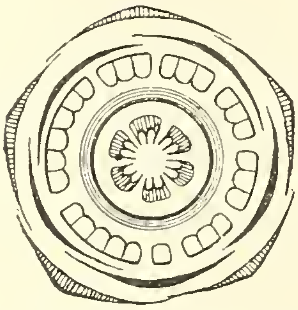


Fig. 554.—Floral diagram of *Citrus vulgaris.* (After EICHLER.)

Family **Rutaceae**.—Flowers usually actinomorphic and four- to five-merous throughout ; stamens in one or two whorls, sometimes as a result of division numerous. Woody plants, rarely herbs, usually with pinnate leaves and WITH ETHEREAL OIL IN NEARLY SPHERICAL INTERCELLULAR CAVITIES (Figs. 552-554).

This large family is almost exclusively restricted to the warm zones. The members of the *Rutaceae* of especial value to man belong to the genus *Citrus*, which differs in many respects from the family type. The *Citrus* species are small, evergreen, and often spinous trees. The leaves are apparently simple, but in reality they are compound leaves reduced to a single leaflet, as is evident from the presence of a segmentation below the lamina, and from a comparison with allied forms. The white, fragrant flowers have a gamosepalous calyx, four to eight thick petals, and numerous stamens united in bundles. The fruit is a multilocular berry with a leathery outer layer full of oil-cavities. All the species of *Citrus* are natives of tropical Asia, but most of them are now cultivated in all warm countries. The most important are—*C. vulgaris*, the Bitter or Seville Orange ; *C. Aurantium*, the Sweet Orange ; *C. Limonum*, the Lemon ; *C. medica*, the Citron.

FIG. 555.—*Quassia amara.* Nat. size.—*OFFICINAL.* (After BERG and SCHMIDT.)

POISONOUS.—*Ruta graveolens.*

OFFICINAL.—*Citrus vulgaris* yields CORTEX FRUCTUS AURANTII and FRUCTUS AURANTII IMMATURI, OLEUM AURANTII FLORUM and FOLIA AURANTII ; *Citrus Limonum*, CORTEX LIMONIS, OLEUM CITRI ; *Citrus Bergamia*, OLEUM BERGAMOTTAE ; *Pilocarpus pennatifolius* (Brazil), FOLIA JABORANDI, PILOCARPINUM ; *Ruta graveolens ;* HERBA RUTAE.

Family **Burseraceae.** — OFFICINAL — MYRRH, the resin of *Commiphora*

Abyssinica and *C. Schimperi*, small East African and Arabian trees. FRANKINCENSE from *Boswellia Carterii* and *B. Bhau-Dajiana* (Arabia, East Africa). ELEMI from *Canarium* sp. (Philippine Islands).

Family **Simarubaceae.**—OFFICINAL—LIGNUM QUASSIAE from *Picrasma* (*Picraena*) *excelsa* (West Indies) and *Quassia amara* (Surinam) (Fig. 555).

Family **Anacardiaceae.**—Species of *Rhus*, are poisonous.

OFFICINAL—MASTICHE, from *Pistacia lentiscus* (Mediterranean).

Family **Zygophyllaceae.**—OFFICINAL—LIGNUM GUIACI and RESINA GUIACI from *Guiacum officinale* (West Indies).

Order 13. Sapindinae

Mostly tropical trees or lianes with obliquely zygomorphic flowers.

Family **Sapindaceae.**—OFFICINAL—GUARANA from *Paullinia Cupana* (= *sorbilis*) (Equatorial Brazil). The small group of the *Hippocastaneae* may be placed here. *Aesculus hippocastanum*, White Horse-Chestnut, occurs from Northern Greece to the Himalayas; *Aesculus pavia*, Pink Horse-Chestnut, North America. Cultivated in Europe,

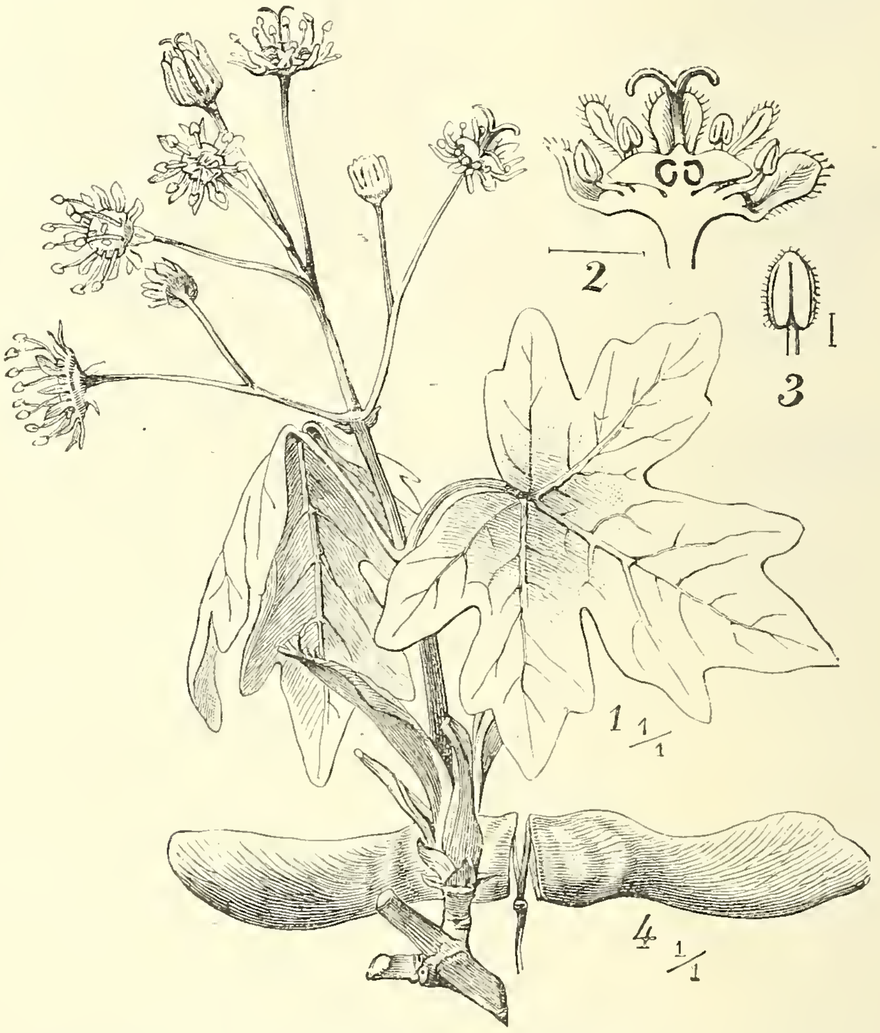


FIG. 556.—*Acer campestre.* 1, Flowering branch; 2, a flower cut through longitudinally; 3, a stamen; 4, the fruit. (After WOSSIDLO.)

Family **Aceraceae.**—The genus *Acer*, Sycamore, occurs in Europe. Trees with actinomorphic flowers, extra-staminal disc; fruit a winged schizocarp. *Acer campestre* (Fig. 556), *A. platanoides*, *A. pseudo-platanus*.

Order 14. Frangulinae

Flowers hypogynous, sometimes perigynous or epigynous, ACTINOMORPHIC, in the perianth and andrœcium three- to four-merous, HAPLOSTEMONOUS, usually with disc; ovary two- to five-merous, septate, with one or two ovules in each loculus; micropyle DIRECTED DOWNWARDS.

The *Frangulinae* comprise, for the most part, shrubs, sometimes growing erect, sometimes climbing by means of tendrils. The leaves are generally simple, in some cases, however, pinnately compound. Although entomophilous, the flowers are characteristically small and inconspicuous, usually with reduced calyx and greenish or white corolla. They have only a single whorl of stamens, which may be placed opposite either the sepals or petals. The fruit is dry or juicy.

FIG. 557.—*Evonymus europaea.* *A*, Flowering branch (reduced); *B*, a flower (magnified); *C*, *D*, the fruit (nat. size).—*POISONOUS.*

Family **Celastraceae**.—Flowers hypogynous; stamens EPISEPALOUS, inserted on a disc; ovary two- to five-locular, with two ovules in each loculus; seeds with coloured ARIL.

Chiefly tropical trees and lianes. *Evonymus europaea,* the Spindle-tree, has poisonous fruits and seeds with a red aril (Figs. 557, 558).

Family **Aquifoliaceae.**—Flowers HYPOGYNOUS; DISC WANTING; ovary two- to five-locular, with one ovule in each loculus; seeds without aril (Fig. 559).

The plants familiarly known as Holly are included in this family, belonging to the genus *Ilex, e.g. I. Aquifolium,* the English Holly. The leaves, known commercially as Paraguay tea (MATÉ), are derived from several sub-tropical South American species of the genus *Ilex.*

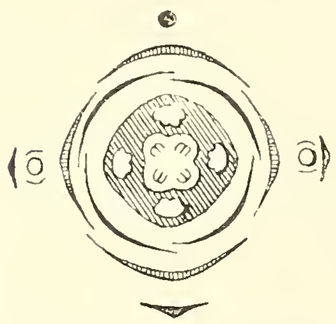


FIG. 558.—Floral diagram of *Evonymous europaea.* (After EICHLER.)

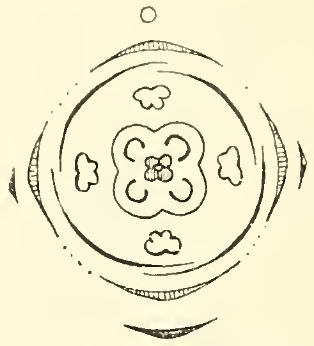


FIG. 559.—Floral diagram of *Ilex aquifolium.* (After EICHLER.)

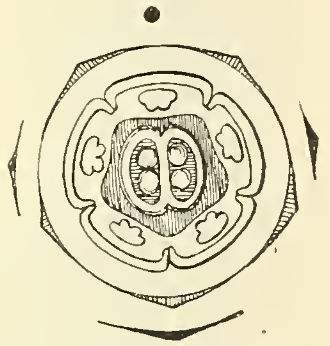


FIG. 560.—Floral diagram of *Ampelopsis hederacea.* (After EICHLER.)

Family **Vitaceae.**—Flowers HYPOGYNOUS; stamens EPIPETALOUS; disc incomplete, consisting of separate glands; ovary generally TWO-LOCULAR; fruit a berry. CLIMBING SHRUBS WITH TENDRILS opposite the leaves (Figs. 560, 561).

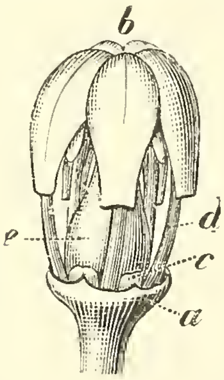


FIG. 561.—*Vitis vinifera.* Flower during its anthesis. *a,* Calyx; *b,* corolla; *c,* disc; *d,* stamens; *e,* ovary (magnified). (After BERG and SCHMIDT.)

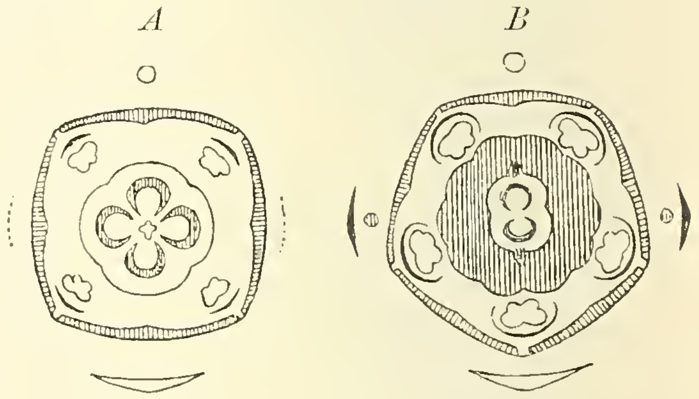


FIG. 562.—Floral diagrams of *A, Rhamnus cathartica;* and *B, Rh. frangula.* (After EICHLER.)

The *Vitaceae* are chiefly indigenous to tropical countries, where many species, particularly of the genus *Cissus,* are common lianes, some of which, when cut, supply a large quantity of clear water. Many species of *Vitis* are natives of North America; *e.g. V. Labrusca,* the Northern Fox-Grape, now largely grown in Europe, and the Virginia Creeper, *Ampelopsis hederacea,* so frequently cultivated as an ornamental climber. *Vitis vinifera,* the Vine, one of the oldest of cultivated plants, grows wild in the temperate regions of Western Asia, Southern Europe, and Northern Africa. The tendrils of the Grape-vine, as is shown by the presence of small leaves or flowers, are metamorphosed shoots. The inflorescence is a profusely branched panicle with pentamerous flowers. The corolla, becoming detached from the flower-axis during the act of flowering, is thrown off in the form of a small star, and is, in consequence, apparently wanting in the opened flowers. The vine has given rise by cultivation to numerous improved varieties and races. Corinthian or dried currants are the small fruits of a seedless variety (var. *apyrena*).

Officinal.—Vinum.

Family **Rhamnaceae.**—Flowers PERIGYNOUS or EPIGYNOUS; petals usually small, often hood-shaped; disc complete; ovary commonly THREE-LOCULAR; fruit a drupe or capsule. Mostly erect, rarely climbing shrubs, chiefly tropical (Figs. 562, 563).

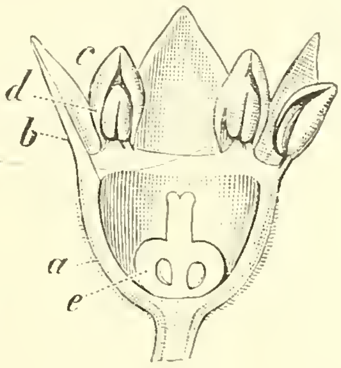


Fig. 563.—*Rhamnus Frangula*. Flower cut through longitudinally. *a*, Receptacle; *b*, calyx; *c*, petal; *d*, a stamen; *e*, pistil (magnified). (After Berg and Schmidt.)

Rhamnus cathartica, the common Buckthorn, is a thorny diœcious shrub with opposite, finely serrate leaves, and unisexual tetramerous flowers producing four-locular drupes. *R. Frangula*, the Alder Buckthorn, has scattered, elliptical, entire leaves, small hermaphrodite flowers (Fig. 563), united in clusters, and black two- to three-locular drupes. Charcoal made from the wood of this species is used in the manufacture of gunpowder.

Officinal.—Fructus Rhamni Catharticae, Cortex Frangulae. Cortex Rhamni Purshianae, from *Rhamnus Purshiana*, native of North America.

The **Buxaceae** differ from other families belonging to the *Frangulinae*, chiefly in having flowers that are either entirely naked or only provided with a simple, floral envelope. The most familiar representative is the Box, *Buxus sempervirens*, a POISONOUS evergreen-shrub frequently cultivated for ornamental borders, etc. To the same alliance belongs also the family **Empetraceae**. *Empetrum nigrum*, the Black Crowberry, is a small heather-like shrub of alpine habit.

Fig. 564.—*Daphne Mezereum* ($\frac{1}{2}$ nat. size).—*Poisonous.*

Order 15. Thymelaeinae

Flowers perigynous, actinomorphic; perianth and andrœcium four- to five-merous; COROLLA REDUCED OR WANTING; one or two whorls of stamens; ovary monomerous, with one ovule. Mostly woody plants.

Family **Thymelaceae.**—Ovule pendulous. The species of *Daphne* are poisonous; *D. Mezereum*, a deciduous shrub, familiar in cultivation, has fragrant, rose-coloured sessile flowers, which make their appearance in the early spring, before the foliage-leaves, on the shoots of the previous year. The fruit is a red berry about the size of a pea (Fig. 564).

OFFICINAL.—CORTEX MEZEREI.

Family **Elaeagnaceae.**—Ovules ERECT; woody plants, WITH SCALY HAIRS. *Hippophaë.*

Order 16. Tricoccae

Family **Euphorbiaceae.**—Flowers hypogynous, actinomorphic, MOSTLY UNISEXUAL; perianth rarely double, USUALLY SIMPLE OR WANTING; andrœcium 1–∞ merous; ovary of three carpels, trilocular, with one or two suspended ovules in each loculus; micropyle DIRECTED UPWARDS AND OUTWARDS, and covered with a fleshy outgrowth (CARUNCLE). Fruit commonly a capsule, whose CARPELS SEPARATE ELASTICALLY FROM A CENTRAL COLUMN (Figs. 565-572).

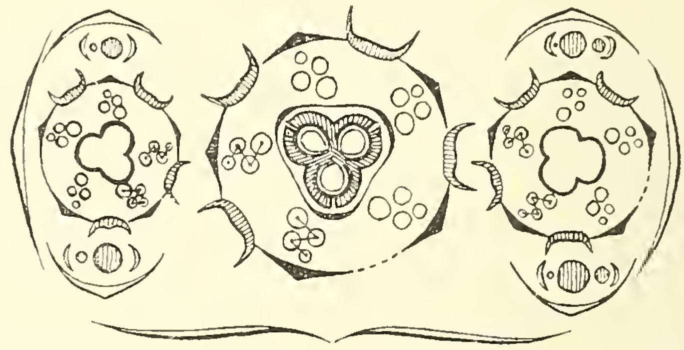


FIG. 565.—Diagram of a dichasial branch of *Euphorbia*, with three cyathia. (After EICHLER.)

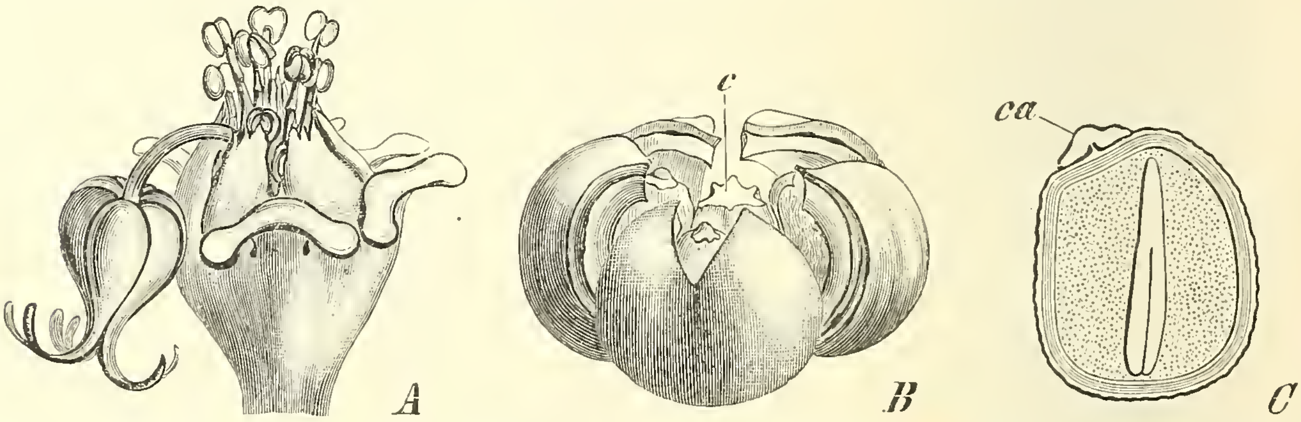


FIG. 566.—*Euphorbia Lathyris.* *A*, Cyathium (× 5); *B*, fruit after dehiscence; *c*, central column (× 2); *C*, seed cut through longitudinally, showing the embryo embedded in the endosperm; *ca*, caruncle (magnified). (After BAILLON.)

The single constant characteristic of the *Tricoccae* is the manner of attachment and structure of the ovule. The *Euphorbiaceae* include plants of the most varied habit, embracing herbs, Cactus-like succulents, shrubs, lianes, and trees, whose leaves may be large, or small, or reduced to scales, or represented by phyllocladia.

The flowers, which individually are always small and inconspicuous, display the same variety in their structure as the vegetative parts. They are sometimes arranged in flower-like inflorescences enveloped by a corollaceous sheath (cf. *Euphorbia*). Although some few species produce dry indehiscent fruits, berries or drupes, the usually trilocular capsules whose carpels or cocci, in dehiscing, separate elastically from a central column (sometimes with great violence, *e.g. Hura crepitans*), and split almost to their base, constitute an easy and certain means of recognising the majority of the *Euphorbiaceae.* In spite of the great variety displayed by the different members, they are so linked together by intermediate forms that this family forms one of the most natural of the vegetable kingdom.

FIG. 567.—*Euphorbia cyparissius* ($\frac{2}{3}$ nat. size). *POISONOUS.*

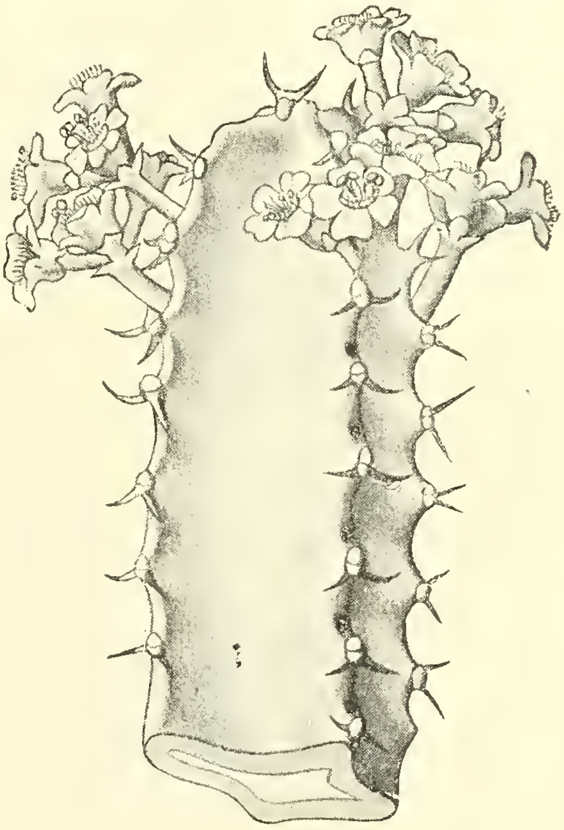


FIG. 568.—*Euphorbia resinifera.*—*OFFICINAL.* (After BERG and SCHMIDT, nat. size.)

REPRESENTATIVE GENERA.—*Euphorbia,* the Spurge (Figs. 565-568). Numerous stalked male flowers, each consisting of a single stamen, and one stalked female flower, are together enveloped by a lobed, bell-shaped involucre, forming an inflorescence termed a CYATHIUM. Such a cyathium resembles a single hermaphrodite flower, particularly when the sheathing involucre is corollaceous. That it, in reality, represents an inflorescence is apparent from the indication of a segmentation visible below each stamen, and also from a comparison with allied genera in which each flower, although otherwise similarly constructed, is provided with a perigone. All the species of *Euphorbia* have unseptated latex-tubes containing a milky juice. *Mercurialis* (Fig. 571): flowers diœcious, with green perigone and dimerous ovaries. *Croton:* all the species of this genus are tropical shrubs with monœcious, heterochlamydeous flowers. *Ricinus* (see under Officinal).

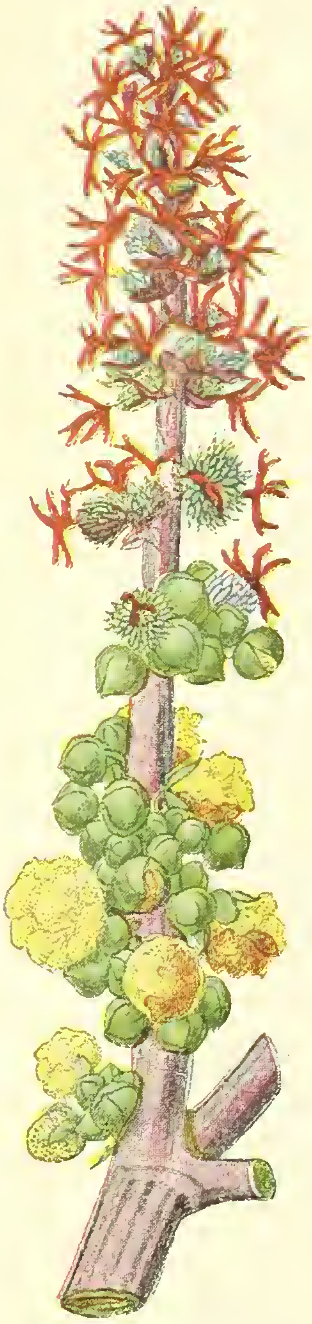


FIG. 569.—*Ricinus communis.* Inflorescence bearing male flowers towards the base and female flowers above. ½ nat. size. (After BERG and SCHMIDT.)

FIG. 570.—*Ricinus communis*, greatly reduced.—*POISONOUS* and *OFFICINAL.* (After BAILLON.)

GEOGRAPHICAL DISTRIBUTION.—The plants of this family are native chiefly of tropical countries, where they occur usually in the form of shrubs, rarely as lianes or trees. CAOUTCHOUC is derived from many of the tropical species, *e.g. Hevea guyanensis* and *H. brasiliensis* (South America). The roots of *Manihot utilissima* (Manioc, Cassava) form an important article of food in the Tropics; from them TAPIOCA is obtained.

Poisonous. — Both the latex and seeds of most *Euphorbiaceae* contain toxic principles. Some species belong to the most poisonous of plants, *e.g.* the tropical

Fig. 571.—*Mercurialis annua.* 1, Branch with male inflorescences ; 2, a male flower ; 3, a stamen ; 4, a female flower ; 5, fruit ; 6, seed ; 7, diagram of female flower ; 8, diagram of male flower.—*Poisonous.* (After Wossidlo ; 2, 3, 4, 5, 6 magnified.)

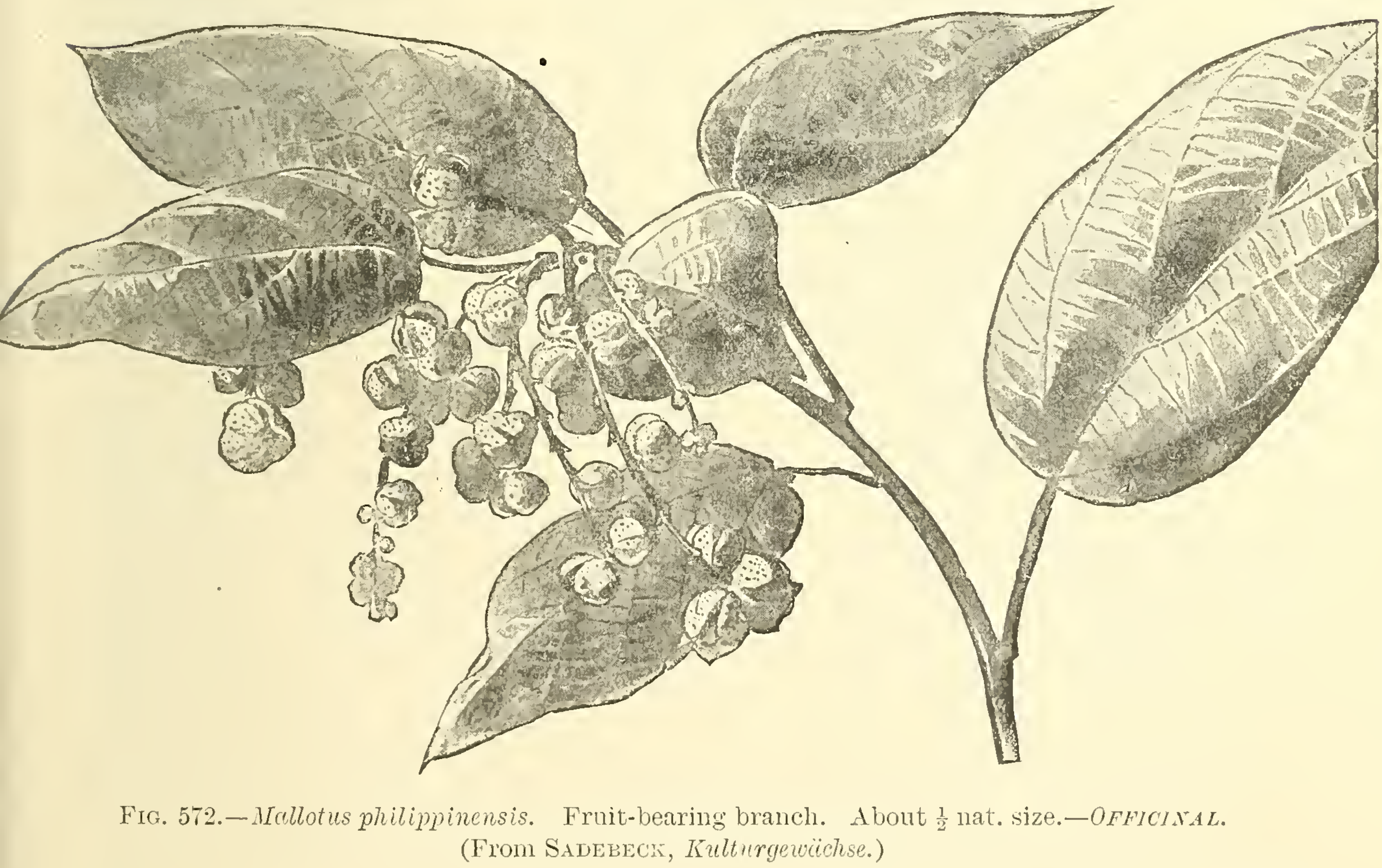


Fig. 572.—*Mallotus philippinensis.* Fruit-bearing branch. About ½ nat. size.—*Officinal.* (From Sadebeck, *Kulturgewächse.*)

American *Hippomane Mancinella*, whose dangerous character, however, has been considerably exaggerated. All the species of *Euphorbia* (Figs. 567, 568), and also, though to a less degree, the species of *Mercurialis* (Fig. 571), are poisonous. The seeds of *Ricinus communis* (the Castor-oil plant, Figs. 569, 570), but not the oil pressed from them, contain a deadly poison.

Officinal.—Euphorbium, from *Euphorbia resinifera*, a Cactus-like shrub growing in Morocco (Fig. 568). Cortex Cascarillae, from *Croton Eleuteria* (Bahama Islands). Oleum Crotonis, from *Croton Tiglium* (East Indies). Kamala, the glandular hairs of the capsules of *Mallotus philippinensis* (Fig. 572), a small tree widely distributed in East Asia and Australia. Oleum Ricini, obtained from the seeds of *Ricinus communis* (Figs. 569, 570). The Castor-oil plant, now so familiar in cultivation, in its native home in Africa is a tree-like plant with large palmately-lobed leaves. The male flowers have branched stamens and occupy the lower, the female the upper part of the axis of the inflorescence. Both kinds of flowers are provided with a simple envelope. The fruit is a three-seeded spinous capsule.

Family **Callitrichaceae**.—Small aquatic plants with unisexual flowers, without perigone; one stamen, one carpel.

Order 17. Umbelliflorae

Flowers actinomorphic, more rarely slightly zygomorphic, epigynous, with a four- to five-merous perianth, HAPLOSTEMONOUS; calyx GREATLY REDUCED; an intra-staminal DISC present; gynœcium usually DIMEROUS; ovary bilocular, with ONE ovule in each loculus; seeds with large endosperm. Herbs and shrubs, commonly WITH HOLLOW AXES; leaves DIVIDED or COMPOUND, usually WITH SHEATHING BASES; flowers SMALL, aggregated in umbels or in umbellate inflorescences.

Fig. 573.—*Cornus mas.* 1, Flowering branch; 2, flower cut through longitudinally; 3, branch with fruit. (After Wossidlo.)

In the structure of their flowers and fruit the *Umbelliflorae* bear a close resemblance on the one side to the few epigynous Frangulinae, on the other, through the *Caprifoliaceae*, to the *Rubiinae*, from which they essentially differ in not having gamopetalous flowers. The union of the members of this group into a natural, systematic order is chiefly based on the similarity exhibited in the form of their inflorescences and on the resemblance existing between their vegetative parts. The designation of the whole order as *Um-*

belliflorae has reference to the umbelliform manner of branching displayed in the floral region; the inflorescences are usually compound umbels, rarely simple umbels or umbellate panicles or cymes. The flowers in most cases are white or yellow. There is a similar correspondence in the vegetative organs. The stems are generally hollow; the leaves are scattered, often very large, usually much divided or compound, and almost always with stalks broadened at the base into a sheath.

Family **Cornaceae.**—Perianth and andrœcium usually tetramerous; petals VALVATE OR IMBRICATED in the bud; gynœcium most often dimerous WITH SIMPLE STYLE; ovary one- to four-locular; fruit a DRUPE OR BERRY (Fig. 573).

FIG. 574.—*Hedera Helix*. 1, Flowering branch; 2, leaf of a sterile branch; 3, flower cut through longitudinally; 4, floral diagram; 5, fruit; 6, seed.—POISONOUS. (After WOSSIDLO.)

This family forms a connecting link between the *Rhamnaceae* and the typical *Umbelliflorae*. It comprises but few herbs, and is usually represented by woody plants with flowers arranged in dichasial inflorescences, and with decussate leaves, which are generally undivided and without a sheath.

Cornus mas and *C. sanguinea* are shrubs, the former sometimes attaining the size of a tree. *C. suecica* is an herb growing in Northern latitudes.

Family **Araliaceae.** — Perianth and andrœcium usually PENTAMEROUS; petals valvate in the bud; gynœcium generally MORE THAN

DIMEROUS; styles most frequently FREE; ovary one to many locular; fruit a DRUPE or BERRY (Fig. 574).

A family of small woody plants with stems either hollow or filled with a spongy pith; rarely solid and woody. The leaves, which are scattered and provided with sheathing bases, are lobed or compound. The flowers are arranged in umbellate or capitate inflorescences, which are frequently aggregated into panicles.

FIG. 575.—*Cicuta virosa.* ½ nat. size. *POISONOUS.*

The *Araliaceae* are found chiefly in tropical Asia, where, in the form of small sparingly-branched trees with large divided leaves and enormous inflorescences of small yellow flowers, they constitute a characteristic part of the vegetation. To this family belongs the Ivy, *Hedera Helix* (Fig. 574), a root-climbing, evergreen shrub, with differently shaped leaves on the fertile and sterile shoots. The berries are POISONOUS.

Family **Umbelliferae.**—Perianth and andrœcium generally pentamerous; petals incurved in the bud; gynœcium DIMEROUS, with FREE STYLES; fruit schizocarpic, usually with OIL-DUCTS. Flowers, with few exceptions, in compound umbels (Figs. 575-581).

The *Umbelliferae* form one of the most natural and easily recognisable plant-families. They are, in the majority of cases, perennial herbs with hollow stems and divided leaves with sheathing bases. The inflorescences are usually compound, and consist of many umbels of small white or yellow, rarely reddish or violet, flowers, which give rise to brownish ribbed, aromatic schizocarps.

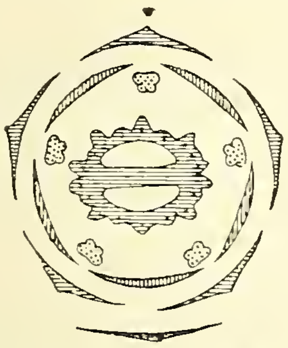


FIG. 576.—*Umbelliferae.* Floral diagram (*Siler*).

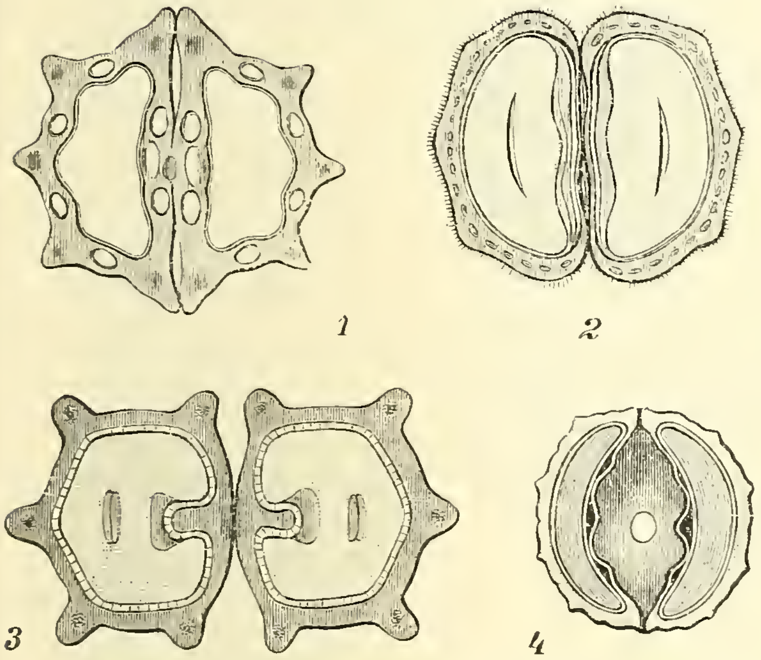


FIG. 577.—Fruit of various *Umbelliferae* in transverse section. 1, *Foeniculum officinale;* 2, *Pimpinella Anisum;* 3, *Conium maculatum;* 4, *Coriandrum sativum.*—*OFFICINAL.* (After BERG and SCHMIDT.)

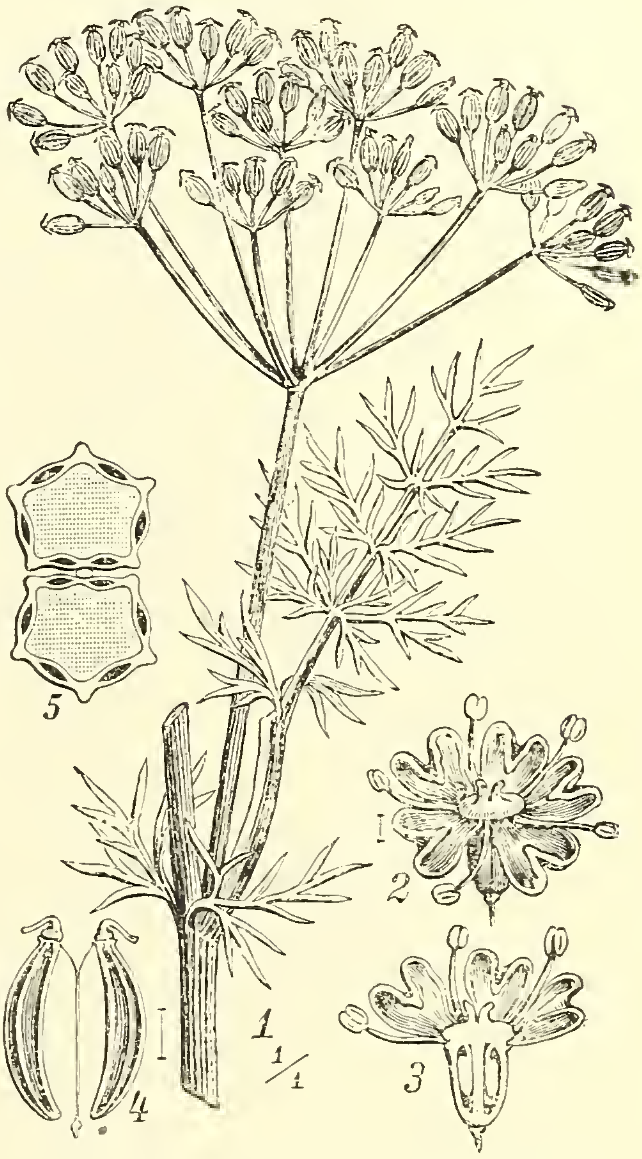


FIG. 578.—*Carum Carvi.* 1, Branch with ripe fruit; 2, a flower; 3, the same cut through longitudinally; 4, fruit; 5, transverse section of fruit.—*OFFICINAL.* (After WOSSIDLO.)

The umbels are often altogether devoid of subtending leaves; where such are present, they form an inconspicuous whorl of bracts, termed an involucre when at the base of the compound umbel, an involucel if subtending the umbellets or secondary umbels (Figs. 580, 581). The presence or absence of involucral whorls is characteristic of different genera, and is, therefore, of great service in distinguishing them.

The following examples may be cited as illustrating deviations from the usual habit: simple entire leaves (*e.g. Bupleurum*); simple umbels (*e.g. Hydrocotyle*); compound inflorescences, paniculate (*e.g. Dorema*); large corollaceous involucres (*e.g. Astrantia, Eryngium*). The most striking variation from the typical habit is the occurrence in temperate South America of *Umbelliferae* with solitary flowers (*Azorella*). All the flowers of an umbel are usually actinomorphic and hermaphrodite. Sometimes, as in *Coriandrum* and *Heracleum* (Cow-Parsnip), the peripheral flowers are zygomorphic; or in some cases the umbel has a central terminal flower of a distinctive colour and size (*e.g. Daucus*), or it may consist in part of unisexual flowers. The calyx is usually barely distinguishable; the petals are provided with a short claw and are obcordate in shape or have incurved apices. The disc consists of two cushion-like swellings and secretes honey. The stamens are incurved in the bud. The styles are short and divergent, with their apices not distinctly thickened.

An exact knowledge of the structure of the fruits is indispensable, as these exhibit the most important distinguishing characters of the species, which in other respects are very much alike (especially poisonous species). The fruits of many species, moreover, are officinal, or are used as spices. The fruit, which is usually small and of varying shape, is a dry schizocarp, and splits when ripe into MERICARPS. It is most frequently somewhat elongated, and circular or elliptical in transverse section; in the latter case, with the major axis either parallel or at right angles to the plane of union of the two carpels. When an elliptical transverse section is very narrow, the fruit is disc-shaped (*Heracleum*). Fruits of a spherical (*Coriandrum*) or double-spherical form (*Bifora*) are more rare. After their separation, the two carpels or mericarps usually remain suspended from a forked stalk, the CARPOPHORE (Fig. 578, 4), until they are eventually detached by the wind. A carpophore is absent in only a few species (*e.g.* the formerly officinal *Oenanthe Phellandrium*). Each mericarp bears on its free surface five longitudinal ridges, enclosing vascular bundles; these are known as the MAIN RIBS (JUGA PRIMARIA). The FURROWS (VALLECULÆ) between the ridges are usually dark-coloured in consequence of the reddish-brown OIL-DUCTS (VITTÆ) which occur immediately below in the tissue of the pericarp (Fig. 577, 1). In many species each of the furrows is traversed by a SECONDARY RIDGE (JUGUM SECUNDARIUM); the prickly fruit, for example, of the common Carrot, *Daucus Carota*, possesses prickly secondary ridges. In many genera (*e.g. Pimpinella*) several oil-ducts occur below each furrow (Fig. 577, 2); in others, the oil-ducts may be present in less than the usual number (*Coriandrum*, Fig. 577, 4) or altogether absent (*Conium*, Fig. 577, 3). The seed completely fills the whole cavity of the mericarp, and is adherent to the pericarp. It contains a large oleaginous endosperm, in the upper part of which the minute embryo, the hypocotyl of which is directed upwards, lies embedded.

According to the form assumed by the endosperm, the following sub-families may be distinguished.

1. *Orthospermeae.*—The endosperm flat, or slightly convex on the ventral side, *i.e.* on the side turned towards the plane of junction of the two mericarps (Fig. 577, 1, 2), *e.g. Hydrocotyle* (Water-Pennywort), *Sanicula* (Sanicle), *Eryngium* (Eryngo), *Cicuta* (Water-Hemlock), *Carum* (Caraway), *Petroselinum* (Parsley), *Pimpinella*, *Sium* (Water-Parsnip), *Bupleurum* (Thorough-wax), *Oenanthe* (Drop-wort), *Aethusa* (Fool's Parsley), *Foeniculum* (Fennel), *Levisticum* (Lovage), *Angelica*, *Archangelica*, *Heracleum* (Cow-Parsnip), *Pastinaca* (Parsnip), *Daucus* (Carrot), etc.

FIG. 579.—*Conium maculatum.* $\frac{1}{2}$ nat. size. OFFICINAL and POISONOUS. To the left the fruit magnified. *m*, ribs ; *k*, furrows ; *c*, line of separation ; *h*, gynophore ; *i*, stigma. (After BERG and SCHMIDT.)

2. *Campylospermeae.*—The ventral side of the endosperm is traversed by a longitudinal groove (Fig. 577, 3) : *e.g. Caucalis* (Bur Parsley), *Torilis* (Hedge Parsley), *Scandix* (Shepherd's Needle), *Anthriscus* (Beaked Parsley), *Chaerophyllum* (Chervil), *Conium* (Hemlock), etc.

3. *Coelospermeae.*—The ventral side of the endosperm is concave, *e.g. Coriandrum*, Coriander (Fig. 577, 4).

GEOGRAPHICAL DISTRIBUTION.—The numerous species of *Umbelliferae* are, for the most part, indigenous to the North Temperate Zone; those occurring in the Tropics grow almost exclusively in the cooler mountainous regions, while the South Temperate Zone possesses some peculiar, abnormally-developed forms. The *Umbelliferae* of the Persian and Thibetan steppes, which attain a height of over 6 feet, contain latex in intercellular spaces of the roots, and are used medicinally in a dry state. Many members of this family are cultivated for culinary purposes. in most cases on account of their aromatic properties; *e.g.* the Common Carrot, *Daucus Carota* var. *sativa;* Celery, *Apium graveolens;* Garden Chervil, *Anthriscus Cerefolium;* Parsley, *Petroselinum sativum;* Dill, *Anethum graveolens;* and also several of the officinal species.

FIG. 580.—*Sium latifolium* (½ nat. size).—*POISONOUS.*

POISONOUS.—*Conium maculatum*, the Poison Hemlock (Fig. 579), a GLABROUS herb, often more than a metre in height, with hollow stems and dull-green decompound leaves. The lower parts of the stems are very frequently, but not always, purple-spotted. The plant is easily recognised by the wavy, crenate ridges of its short, laterally compressed fruit, and also by its disagreeable odour when bruised (resembling that of mice). *Cicuta virosa*, the Water-Hemlock (Fig. 575), a large herb growing along the edges of ponds and ditches, is one of the most dangerous of poisonous plants. It has a turnip-like white RHIZOME FULL OF INTERNAL CAVITIES, and large tripinnate leaves with narrow lanceolate, serrate leaflets. The small white flowers are aggregated in compound umbels and produce subglobose fruits. *Berula angustifolia* and the different species of *Sium* and *Oenanthe* are less poisonous; they are all marsh or aquatic plants. The last-named genus is easily distinguishable by the absence of a carpophore. *Sium latifolium* (Fig. 580), which is frequently found in company with the Water-Hemlock, has simply pinnate leaves with lanceolate, sharply serrate leaflets. The Fool's Parsley, *Aethusa Cynapium* (Fig. 581), a common weed in gardens, produces an intoxicating effect when eaten. It differs from the true parsley in having white instead of yellow flowers, ONE-SIDED, THREE-LEAVED (instead of six- to eight-leaved) INVOLUCELS, and an odour of garlic.

FIG. 581.—*Aethusa Cynapium* ($\frac{2}{3}$ nat. size).—*POISONOUS.*

OFFICINAL.—*Archangelica officinalis* yields RADIX ANGELICAE; *Levisticum officinale*, RAD. LEVISTICI; *Pimpinella magna* and *P. Saxifraga*, RAD. PIMPINELLAE; *Imperatoria Ostruthium*, RHIZOMA IMPERATORIAE; *Pimpinella Anisum* (Anise), FRUCTUS ANISI, OLEUM ANISI; *Foeniculum capillaceum*, FRUCTUS FOENICULI, OLEUM FOENICULI; *Carum Carvi* (Caraway), FRUCTUS CARVI, OLEUM CARVI; *Coriandrum sativum*, FRUCTUS CORIANDRI; *Petroselinum sativum*, FRUCTUS PETROSELINI; *Conium maculatum*, HERBA CONII; *Dorema Ammoniacum* (Persia), AMMONIACUM; *Ferula galbaniflua* (Persia), GALBANUM; *Ferula Narthex* (Persia) and *F. Asafoetida*, ASAFOETIDA.

Order 18. Saxifraginae

Flowers hypogynous, perigynous or epigynous, actinomorphic, in perianth and andrœcium pentamerous; stamens usually OBDIPLOSTEMONOUS; gynœcium two- to five-merous, syncarpous or apocarpous; seeds generally ALBUMINOUS.

This order is somewhat artificial, and difficult to characterise, as it consists of members which exhibit a great diversity in the structure of their flowers. It cannot be sharply separated from the *Rosiflorae;* and as it stands also in close affinity with the *Cystiflorae*, *Myrtiflorae*, and *Ericinae*, it may be regarded as constituting an intermediate group uniting all these different alliances.

Family **Crassulaceae.**—Flowers hypogynous or epigynous, hermaphrodite, with a variable number of members in the different whorls; perianth differentiated into calyx and corolla; andrœcium obdiplostemonous or haplostemonous; carpels FREE or slightly united, with GLANDULAR SCALES (DISC), one at the base of each carpel; capsules containing numerous small seeds with little or no endosperm. Succulent herbs and undershrubs (Fig. 582).

Fig. 582.—*Sedum Telephium.* *a*, Flower; *b*, flower in longitudinal section. (×4.)

The members of this family are easily recognisable by their fleshy, entire leaves. Their flowers are usually bright yellow or red in colour, and are arranged in cymose inflorescences.

Geographical Distribution.—The *Crassulaceae*, like all succulents, thrive best in dry, sunny situations. They are almost universally found on rocks, walls, and roofs. The genus *Sedum* has usually pentamerous flowers: *Sedum acre*, the Mossy Stonecrop, grows on walls and rocks, as does also *S. Telephium*, the Garden Orpine or Live-for-ever. The flowers of the genus *Sempervivum* are 6-∞ merous. *S. tectorum*, the Houseleek, and other species are frequently cultivated.

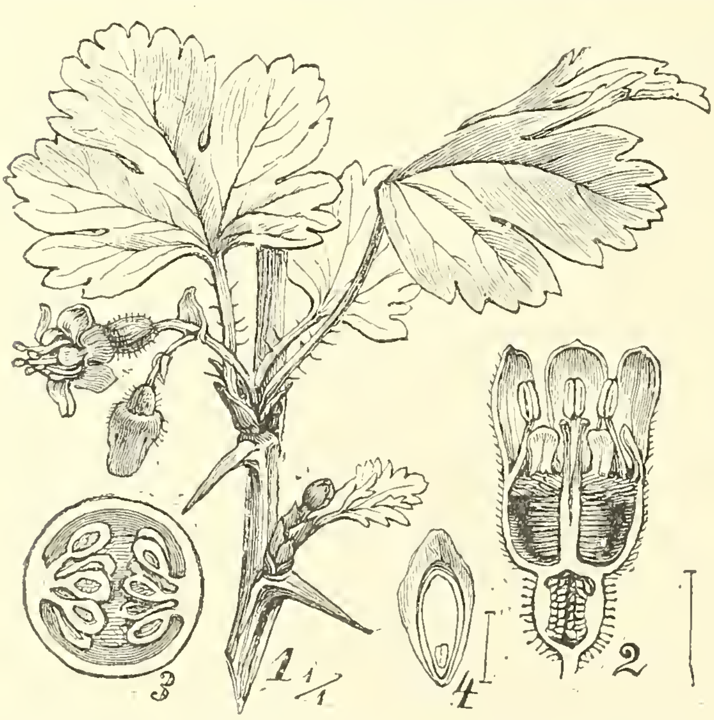


Fig. 583.—*Ribes Grossularia.* 1, Flowering branch; 2, flower cut through longitudinally; 3, fruit in transverse section; 4, longitudinal section of seed. (After Wossidlo.)

Family **Saxifragaceae.**—Flowers perigynous or epigynous, hermaphrodite, with calyx and corolla; stamens obdiplostemonous or haplostemonous;

carpels, usually two, WITHOUT scales, and UNITED, either wholly or only at the base. Fruit usually a capsule, containing numerous small seeds with abundant endosperm (Fig. 583).

The *Saxifragaceae* comprise a number of herbs and woody plants very unlike in appearance. The flowers are small, or at most only medium-sized and aggregated into inflorescences.

GEOGRAPHICAL DISTRIBUTION.—In Northern Europe the genus *Saxifraga* is widely represented by numerous species on the rocks and boulders of mountains. Most of the members of this family are found in the Temperate Zone, although a relatively large number occur also in the Arctic regions; *Saxifraga granulata*, *S. tridactylites*, and *Parnassia palustris* are representatives of the family in the plains. Several species of the genus *Ribes* are cultivated for the sake of their fruit (*e.g. R. rubrum*, the Red Currant; *R. nigrum*, the Black Currant; *R. Grossularia*, the Gooseberry); while other species of the same genus and other genera are frequently used as ornamental plants (*Saxifraga*, *Hydrangea*, *Philadelphus*, *Deutzia*).

OFFICINAL.—SYRUPUS RIBIUM from *Ribes rubrum*.

The **Hamamelidaceae**, a sub-tropical family of woody plants with apetalous flowers, are very closely allied to the *Saxifragaceae*.—OFFICINAL: STYRAX LIQUIDUS, obtained from the balsam-canals in the cortex of *Liquidambar orientalis*.

Family **Platanaceae**.—Flowers MONŒCIOUS, with RUDIMENTARY PERIANTH; the male with REDUCED andrœcium; the female perigynous, with free carpels. Seeds without endosperm. This family includes only the single genus *Platanus*, with but four species, all of which are trees with scaly bark, palmately lobed leaves, and sheathing connate stipules. The flowers, which are small and insignificant, are clustered into spherical heads with long stalks; the fruit is a nut. *Platanus orientalis*, from Western Asia, and *P. occidentalis*, the American Plane-tree, are frequently grown as shade-trees.

Order 19. Rosiflorae

Including the single family **Rosaceae**.—Flowers perigynous or epigynous, almost always actinomorphic; perianth generally pentamerous; stamens usually MORE NUMEROUS than the perianth leaves; gynœcium in perigynous flowers entirely APOCARPOUS, in epigynous flowers with at least the upper part of the carpels free; seeds WITHOUT ENDOSPERM. Leaves ALTERNATE, STIPULATE (Figs. 584-591).

The flowers of the *Rosaceae* may in all cases be derived without difficulty from the typical Dicotyledonous type, although it is shown in an unmodified form in only a few genera, *e.g.* in *Quillaja* (Fig. 589), whose flowers are constructed of five pentamerous whorls. The flowers of most of the species are characterised by the possession of an indefinite number of stamens, as a result of the splitting of the whorls and of the individual members of the andrœcium. A similar multiplication of the parts is also of frequent occurrence in the gynœcium. A Rose with its numerous stamens and apocarpous gynœcium consisting of numerous carpels may serve as the type of the flowers of the *Rosaceae* (Fig. 584, *C*). Similar polyandrous, apocarpous flowers are characteristic of the *Ranunculaceae*, but, as they are hypogynous and have the parts arranged spirally, they differ greatly from those of the *Rosaceae*. On the other hand, although less frequently, the flowers of this family may suffer a reduction of their parts (Fig. 584, *D*). Thus in the flowers of the genus *Alchemilla* the inner whorl of the perianth is wanting; the andrœcium is also not unfrequently reduced to a single whorl, in *Alchemilla arvensis* even to a single stamen, while in the *Prunoideae* the gynœcium consists similarly of but a single carpel. Such reduced and modified flowers are linked to those with the typical or greater number of parts by all possible transitional

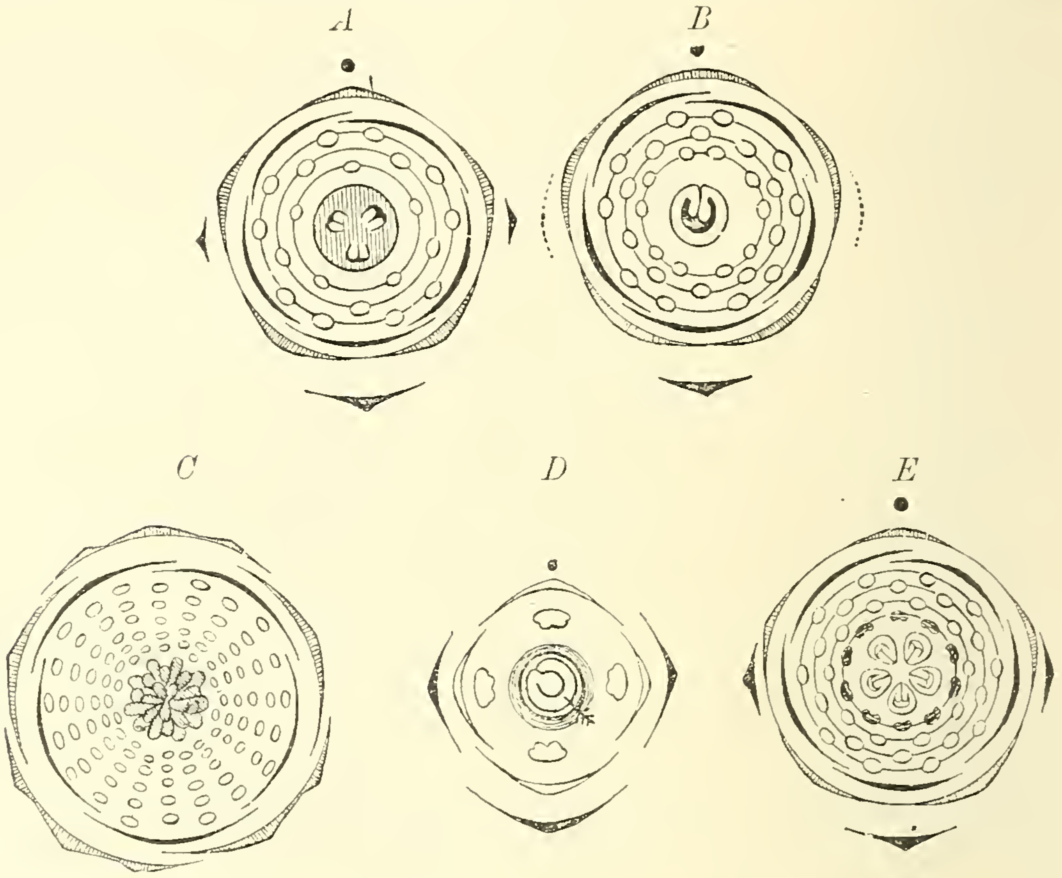


Fig. 584.—Floral diagrams of *Rosaceae*. *A*, *Sorbus domestica*; *B*, *Prunus Padus*; *C*, *Rosa tomentosa*; *D*, *Sanguisorba officinalis*; *E*, *Spiraea hypericifolia*. (After Eichler.)

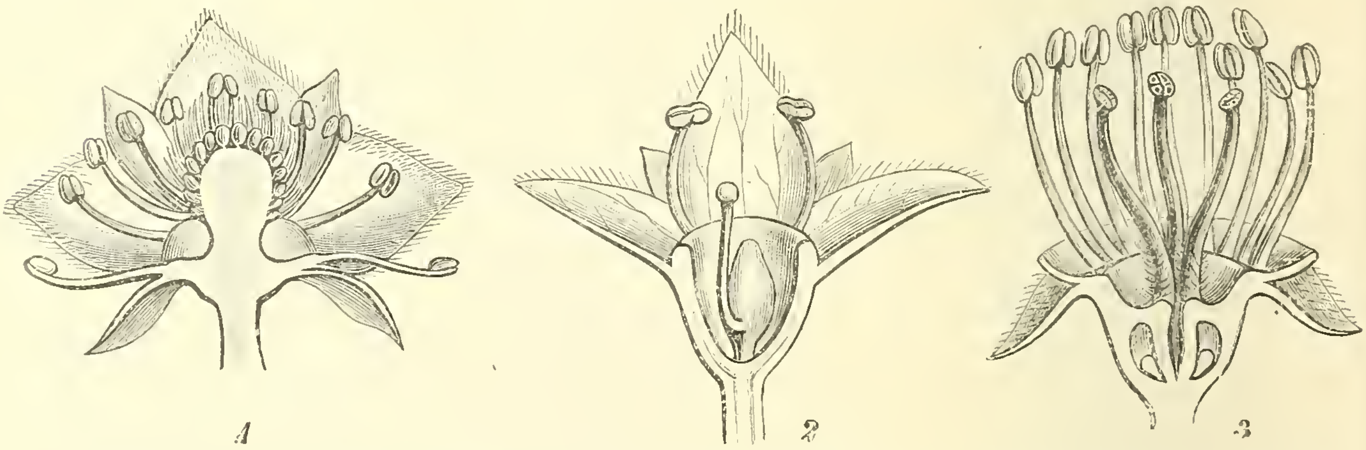


Fig. 585.—*Rosaceae*. Three flowers cut through longitudinally to show different forms of receptacles. 1, *Comarum palustre*; 2, *Alchemilla alpina*; 3, *Pirus malus*. (After Focke in *Natürl. Pflanzenfamilien*.)

forms. The greater or less degree of expansion exhibited by the floral axis, to which in particular the perigynous and epigynous character of the flowers of the *Rosaceae* is due, has been in large measure the cause of the variability displayed by Rosaceous flowers (Fig. 585). In the simplest cases the receptacle is flat or cushion-shaped, as in many species of *Potentilla*, and bears the perianth-leaves and stamens on its margin, while the carpels are inserted on its surface. In other cases, as in the Strawberry and Raspberry, the central portion of the receptacle is prolonged into a club-shaped protuberance to which the carpels are attached (Fig. 585, 1). In other cases, again, the receptacle is extremely concave, cupular in *Prunus* and *Alchemilla* (Fig. 585, 2), urn-shaped in the genus *Rosa*. The epigynous flowers, such as those of the Apple (Fig. 585, 3), differ from the perigynous flowers with concave receptacles, in that the carpels are adnate to the wall of the receptacle.

FIG. 586.—*Pirus communis.* 1, Flowering branch; 2, a flower cut through longitudinally; 3, longitudinal section of fruit; 4, floral diagram. (After WOSSIDLO.)

The fruit is sometimes dry, sometimes fleshy. If, in conformity with the more usual custom, only the product developed from the carpels after fertilisation is termed a fruit, a Strawberry must be regarded as a collection of numerous nutlets or achenes, and an Apple as a spurious fruit. According to the definition of a fruit which has been adopted in this book, in which the conception of the term fruit is made to correspond with that of the flower, the receptacle, as being part of the flower, may also take part in the formation of the fruit. The Strawberry may thus be regarded as a juicy fruit with dry, superficial carpels; while the Apple may be described as a berry. In other cases the fruit is capsular as in *Spiraea*, or nut-like as in *Poterium*.

The *Rosaceae* are herbs or more frequently woody plants, usually with conspicuous flowers. Their leaves are very often pinnate, with toothed leaflets; when simple they are, as a rule, serrate or lobed, rarely entire. The stipules, which are scarcely ever absent, are sometimes herbaceous, sometimes scale-like.

FIG. 587.—*Rubus fruticosus.* 1, Flowering branch; 2, longitudinal section of a flower; 3, fruit; 4, floral diagram. (After WOSSIDLO.)

SUB-FAMILIES.—1. *Pomoideae* (Fig. 586).—Flowers epigynous; fruit a berry. (*a*) Carpels in the fruit parchment-like: *Pirus* (incl. *Sorbus*) with two ovules, *Cydonia* with numerous ovules in each carpel. (*b*) Carpels in the fruit hard and stone-like: *Mespilus*, *Crataegus*.

2. *Rosoideae* (Fig. 584, *C*, *D*).—Flowers perigynous; carpels enclosed in the fruit by the receptacle. (*a*) Receptacle becoming hard in the fruit; flowers tetramerous, small, destitute of corolla: *Poterium*, polygamous with anemophilous flowers in capitate inflorescences; *Sanguisorba*, resembling *Poterium*, but the flowers are entomophilous, and hermaphrodite; *Alchemilla*, flowers with epicalyx.

(*b*) Receptacle as in (*a*), flowers pentamerous, with corolla : *Agrimonia*, *Hagenia*.
(*c*) Receptacle fleshy, flowers with corolla : *Rosa*.

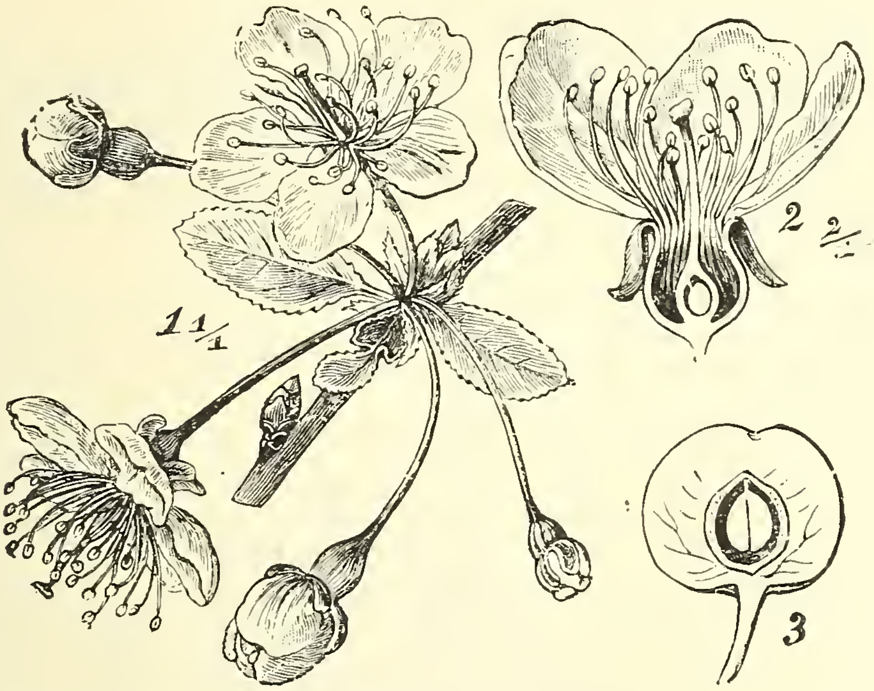


FIG. 588.—*Prunus Cerasus*. 1, Flowering branch ; 2, a flower cut through longitudinally ; 3, fruit in longitudinal section. (After WOSSIDLO.)

3. *Ruboideae* (Fig. 587).—Flowers perigynous ; receptacle flat or convex, with numerous indehiscent carpels : *Potentilla*, with dry fruit ; *Fragaria*, fruit when ripe consisting of a fleshy receptacle with dry carpels ; *Rubus*, carpels drupaceous.

4. *Spiraeoideae* (Fig. 584, *E*).—Flowers perigynous ; receptacle concave ; carpels few, when ripe capsular and many-seeded : *Spiraea*, *Quillaja*.

5. *Prunoideae* (Figs. 584, *B* ; 588).—Flowers perigynous, with one carpel ; fruit a drupe : *Prunus*.

6. *Chrysobalanoideae*. — Flowers frequently zygomorphic.

FIG. 589.—*Quillaja Saponaria*. OFFICINAL. (After SCHUMANN and ARTHUR MEYER.)

GEOGRAPHICAL DISTRIBUTION.—The *Rosaceae*, although distributed over the whole globe, are chiefly represented in the Temperate Zone ; in the Tropics, with the exception of the *Chrysobalanoideae*, they are confined almost entirely to the high mountainous regions. The *Rosaceae* have contributed largely to the list of cultivated plants : the Pear, *Pirus communis ;* the Apple, *Pirus Malus ;* the Quince, *Cydonia vulgaris ;* the Medlar, *Mespilus germanica ;* the Strawberry, species of *Fragaria ;* the Raspberry, Blackberry, etc., species of *Rubus ;* the Wild Cherry, *Prunus avium ;* the Dwarf or

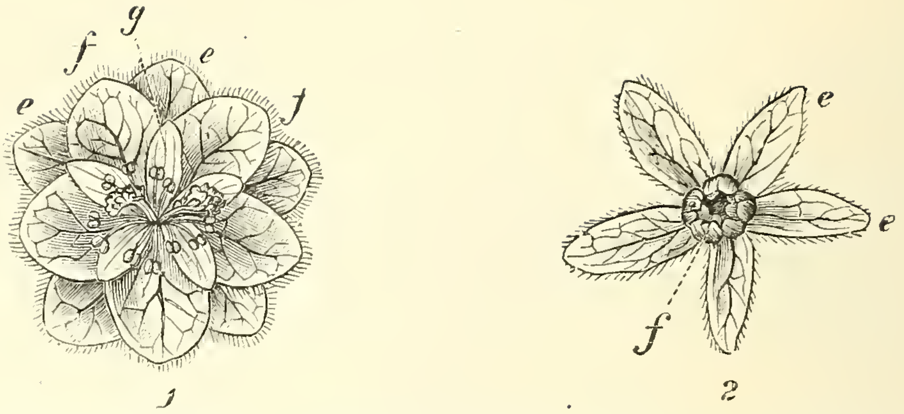


Fig. 590.—*Hagenia abyssinica.* 1, Flower ; *e*, epicalyx ; *f*, calyx ; *g*, corolla (× 4) ; 2, fruit (nat. size), with enlarged epicalyx.—*OFFICINAL.* (After Berg and Schmidt.)

Fig. 591.—*Hagenia abyssinica.* Inflorescence ($\frac{1}{2}$ nat. size).—*OFFICINAL.* (After Berg and Schmidt.)

Morello Cherry, *Pr. Cerasus;* the Wild Plum, *Pr. domestica;* the Bullace Plum, *Pr. insititia;* the Apricot, *Pr. armeniaca;* the Peach, *Pr. persica;* the Almond, *Pr. Amygdalus.* The *Rosaceae* include also many ornamental plants, *e.g.* various species of *Rosa*, *Crataegus*, *Potentilla*, *Rubus*, *Spiraea*, *Kerria*, *Prunus*, etc.

POISONOUS.—The seeds of many species contain prussic acid, although usually not in dangerous quantities, if eaten when first ripe. The leaves of the Cherry-Laurel (*Prunus Laurocerasus*) also contain prussic acid, and when eaten they act as a poison.

OFFICINAL.—*Cydonia vulgaris* affords SEMEN CYDONIAE and MUCILAGO CYDONIAE. *Hagenia abyssinica* (a diœcious tree native of Abyssinia, with greenish female flowers whose epicalyx and calyx turn red after fertilisation) yields FLORES KOSO (Figs. 590, 591). FLORES ROSAE, OLEUM ROSAE from *Rosa centifolia;* SYRUPUS RUBI IDAEI from *Rubus idaeus;* AMYGDALAE DULCES, AMYGDALAE AMARAE, and OLEUM AMYGDALARUM from *Prunus Amygdalus;* PULPA PRUNORUM from *Pr. domestica;* AQUA LAUROCERASI from *Pr. Laurocerasus;* SYRUPUS CERASORUM from *Prunus Cerasus;* *Quillaja Saponaria* (an evergreen diœcious tree indigenous to Chili and Peru (Fig. 589) yields CORTEX QUILLAJAE; FLOS SPIREAE from *Spiraea ulmaria;* FOLIUM RUBI FRUTICOSI from *Rubus fruticosus;* RHIZOMA TORMENTILLAE from *Potentilla tormentilla.*

Order 20. Leguminosae

Flowers HYPOGYNOUS or slightly PERIGYNOUS, actinomorphic, or more frequently zygomorphic; perianth usually pentamerous; median sepal anterior; andrœcium diplostemonous, rarely consisting of an indefinite or reduced number of stamens; gynœcium of one carpel, generally WITH MANY OVULES ATTACHED, IN TWO ROWS, TO THE VENTRAL SUTURE; fruit usually a LEGUME. Seeds mostly without albumen. Leaves generally COMPOUND, STIPULATE.

The *Leguminosae*, with actinomorphic flowers, resemble the monocarpellary *Rosaceae*, but they may be distinguished from them by their unexpanded or only slightly enlarged receptacles, and by their fruit.

The structure of the flower is also as varied in the *Leguminosae* as in the *Rosiflorae.* The *Mimosaceae* have actinomorphic flowers; those of the *Caesalpiniaceae* are sometimes only slightly irregular, sometimes more distinctly zygomorphic, leading by gradual transition to the highly zygomorphic flowers of the *Papilionaceae.* These differences in the structure of the flowers are chiefly due to the various forms assumed by the corolla, in part also to the unequal development of the andrœcium. The stamens are sometimes straight, sometimes curved, united or free, usually ten in number, but at times reduced by suppression or increased by division. On the other hand, the gynœcium and flower-axis, to the variability of which the diversity of form exhibited by the flowers of the *Rosiflorae* is so largely due, are very uniformly developed in the *Leguminosae*, and take but small part in the various modifications met with in the structure of the flowers.

Unlike the flowers, the fruit of the *Leguminosae* almost always presents the same structure. In the majority of cases it is a many-seeded legume, rarely a dry indehiscent fruit, or it may be a berry or drupe. Even when thus modified, all the forms of the fruit bear a certain degree of resemblance to each other.

Fig. 592.—*Acacia Catechu* (½ nat. size).—*Officinal.* (After Berg and Schmidt.)

The inflorescences are most generally racemose; racemes, spikes or capitula, with in all cases lateral flowers. The leaves are scattered, usually pinnate or bipinnate, with leaflets either entire or slightly toothed, never deeply lobed or incised. Simple leaves are of rare occurrence in this order, and are usually small.

Just as in most of the more natural orders, the attempt to divide the *Leguminosae* into families is attended with difficulty, as the extreme forms are linked together by all possible intermediate stages. The whole order is in consequence sometimes regarded as a single family, in which the main groups take the position of sub-families. In their typical representatives, however, these groups are so characteristically developed that it seems best to consider them as distinct families.

Family **Mimosaceae**.—Flowers ACTINOMORPHIC; corolla absent, or if present, with petals VALVATE in the bud; andrœcium haplostemonous, diplostemonous, or polystemonous, USUALLY WITH FREE STAMENS; embryo straight (Figs. 592-594).

Fig. 593.—*Acacia Senegal*. Flowering branch (nat. size).—OFFICINAL. (After A. Meyer and Schumann.)

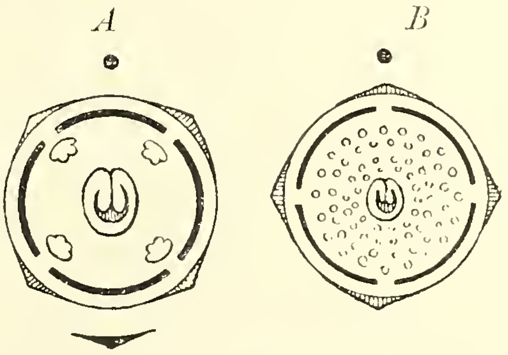


Fig. 594.—Floral diagrams of *Mimosaceae*. *A*, *Mimosa pudica*; *B*, *Acacia lophantha*. (After Eichler.)

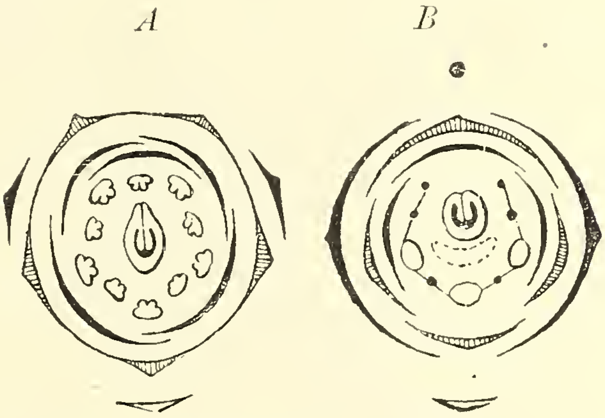


Fig. 595.—Floral diagrams of *Caesalpiniaceae*. *A*, *Cercis siliquastrum*; *B*, *Tamarindus indica*. (After Eichler.)

This family consists for the most part of shrubs, lianes or small trees, with doubly pinnate leaves, or, as in many Australian species, with phyllodia. The flowers are small, in dense heads or spikes, whose bright, usually yellow, colour is due to the long stamens which project beyond the inconspicuous perianth. The more important genera are *Acacia* and *Mimosa*. Both genera are largely represented in the Tropics. *Mimosa pudica*, the Sensitive Plant, is a troublesome and worthless weed. In Australia the *Mimosaceae* occupy an important position, and together with Eucalyptus trees they form the chief part of all the woody vegetation, while in the dry regions of South Africa, in the form of thorny shrubs (*e.g.* *Acacia horrida*), they often constitute the only woody plants. Acacias are largely cultivated as ornamental trees in the Mediterranean region.

FIG. 596.—*Krameria triandra* (nat. size).—OFFICINAL. (After BERG and SCHMIDT.)

FIG. 597.—*Cassia acutifolia.* Leaf and inflorescence —OFFICINAL. (After BERG and SCHMIDT.)

FIG. 598.—*Tamarindus indica* (nat. size).—OFFICINAL. (After BERG and SCHMIDT.)

Officinal.—*Acacia Senegal*, a shrub native of the Nile countries and Senegal, yields Gummi arabicum. The gum, which is formed by the disorganisation of the stem-parenchyma, exudes as a thick fluid from wounds in the stems, and afterwards hardens (Fig. 593). Catechu is an extract made from the heart-wood of *Acacia Catechu* (Fig. 592) and *A. Suma* (East Indian trees).

Fig. 599.—*Copaifera Langsdorffii* (½ nat. size).—*Officinal.* (After Berg and Schmidt.)

Family **Caesalpiniaceae.**—Flowers more or less ZYGOMORPHIC; corolla sometimes absent, when present, NOT AT ALL OR ONLY IMPERFECTLY PAPILIONACEOUS, with ASCENDING IMBRICATE ÆSTIVATION (*i.e.* the posterior petal overlapped by the others); andrœcium with FREE STAMENS, often REDUCED. Embryo STRAIGHT (Figs. 595-600).

The *Caesalpiniaceae* are shrubs or trees, and, unlike the *Papilionaceae*, often have bipinnate leaves. The flowers may be large or small. Their corolla is variously constructed, sometimes actinomorphic (*e.g. Cassia*, the zygomorphic character of whose flowers is due to the andrœcium), sometimes strongly zygomorphic

(*Tamarindus*), but very rarely somewhat papilionaceous (*Cercis Siliquastrum*). The members of this family, whose largest genus is *Cassia*, are almost exclusively tropical. The coloured heart-wood of many species gives them a great technical value (Logwood from *Haematoxylon campechianum*, Pernambuco or Brazil Wood from *Caesalpinia brasiliensis*). The Judas-tree (*Cercis Siliquastrum*) from Southern Europe (with flowers springing directly from the stem), and the Honey Locust (*Gleditschia triacanthos*) from North America, are often cultivated in parks and gardens.

Officinal.—Folia Sennae, the leaflets of *Cassia angustifolia* (from tropical East Africa and Arabia). Folia Sennae Alexandrinae, from *C. acutifolia* (Fig. 597). The officinal species of *Cassia* are shrubs with yellow-flowered racemes (Fig. 597). *Cassia fistula* (Tropical America), Fructus Cassiae Fistulae and Pulpa Cassiae Fistulae. *Cassia obovata* (Egypt), Fructus Sennae. The balsam-canals in the wood of *Copaifera guianensis* (Fig. 599) and other species (trees of tropical America) contain Balsamum copaivae. Rhatany Root, Rad. Ratanhiae, is obtained from *Krameria triandra*, a Peruvian shrub. Lignum Haematoxyli is the heart-wood of *Haematoxylon campechianum* (South America). Pulpa Tamarindorum is the preserved fleshy mesocarp of the fruit of the Tamarind-tree, *Tamarindus indica* (Figs. 598, 600).

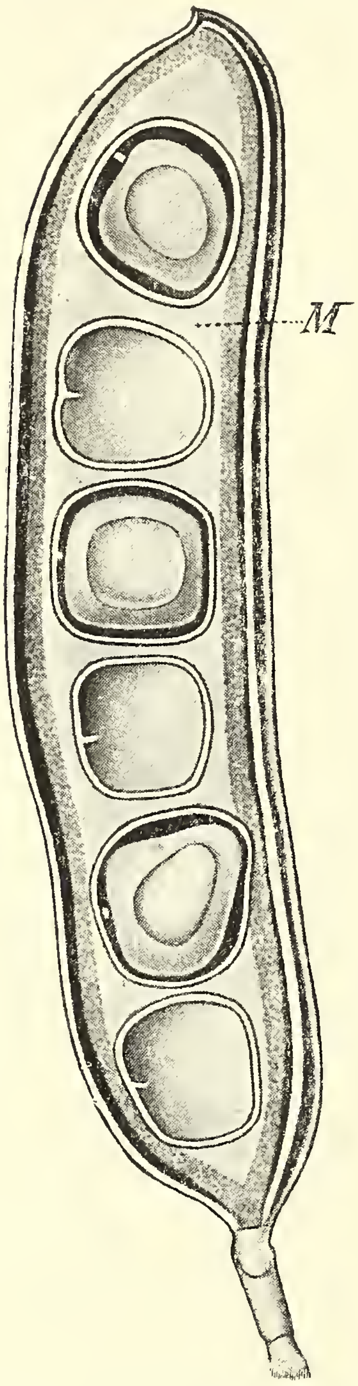


Fig. 600.—*Tamarindus indica.* Fruit in longitudinal section. *M*, The fleshy mesocarp.—*Officinal.* (After Berg and Schmidt.)

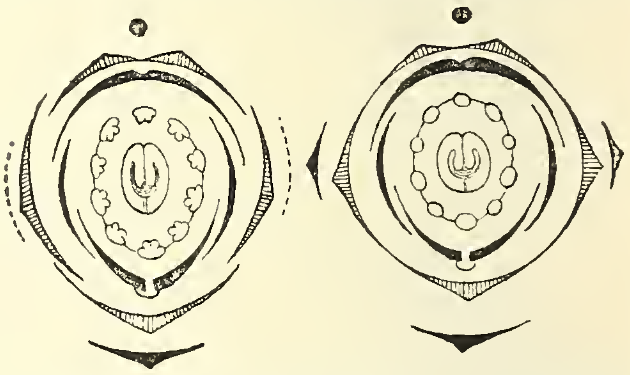


Fig. 601.—Floral diagrams of *Papilionaceae.* *A*, *Vicia Faba*; *B*, *Cytisus laburnum.* (After Eichler).

Family **Papilionaceae.**—Flowers strongly ZYGOMORPHIC, PAPILIONACEOUS; corolla with descending IMBRICATE ÆSTIVATION (*i.e.* the posterior petal enclosing the others in the bud); androecium always diplostemonous, monadelphous or more frequently DIADELPHOUS, the posterior stamen being free; the embryo curved (Figs. 601-608).

The *Papilionaceae* comprise both herbs and woody plants; many are stem- or tendril-climbers. The leaves are generally oddly pinnate. The flowers are usually disposed in racemes, more rarely in heads;

except in some few genera which approach more nearly the *Caesalpiniaceae* (*e.g. Toluifera*), they are characterised by papilionaceous

Fig. 602.—*Lotus corniculatus.* 1, Flowering branch; 2, a flower; 3, andrœcium and gynœcium; 4, carpel; 5, fruit; 6, corolla; *a*, standard; *b*, wings; *c*, keel; 7, floral diagram. (After Wossidlo.)

corollas (Fig. 602). The posterior petal is much enlarged and is termed the STANDARD (VEXILLUM); the two lateral petals represent the WINGS (ALÆ), while the two anterior are usually united by their lower margins, and together form the KEEL (CARINA). In the bud the wings are enclosed by the standard, the keel by the wings (DESCENDING IMBRICATE ÆSTIVATION); in the *Caesalpiniaceae* the æstivation is in exactly the reverse order (ASCENDING). The stamens in most cases curve upwards. The cohesion of the filaments does not generally extend throughout their whole length, so that their upper ends are usually free. Stamens wholly free are found only in a few exceptional genera, such as *Toluifera*. The legumes commonly have a parchment-like wall; dry indehiscent fruits rarely occur in this family; succulent fruits never.

Fig. 603.—*Toluifera Pereirae.* An anomalous papilionaceous flower. One petal (the standard) enlarged, the others small. Stamens only united at the base.—*Officinal.* (Enlarged. After Berg and Schmidt.)

Sub-Families.—1. *Genistoideae.*—Leaves entire, simple or pinnate, stamens usually united. *Lupinus* (Lupine), *Cytisus* (Laburnum), *Genista.*

2. *Trifolioideae.*—Leaves usually pinnate with toothed leaflets, fruit indehiscent. *Trifolium* (Clover, Trefoil), with persistent perianth; *Medicago* (Medick), with deciduous corolla and sickle-shaped or spirally-twisted legumes; *Trigonella* (Trigonel); *Melilotus* (Melilot, Sweet Clover), with flowers in loose racemes and small, elongated or globular legumes; *Ononis* (Rest-Harrow), with monadelphous stamens.

Fig. 604.—*Coronilla varia* (nat. size).—*Poisonous.*

3. *Lotoideae.*—Stamens diadelphous. *Anthyllis* (Kidney-Vetch); *Lotus* (Bird's-foot Trefoil), etc.

4. *Galegoideae.*—Leaves imparipinnate. *Astragalus* (Milk-Vetch), with legumes imperfectly separated by a false dissepiment; *Robinia* (Locust-tree), etc.

5. *Hedysaroideae.*—Stamens diadelphous; fruit a jointed legume or lomentum. *Coronilla*, *Hedysarum*, *Desmodium* (Tick-Trefoil); *Onobrychis* (Sainfoin); *Arachis* (*A. hypogaea*, the Pea-nut), etc.

6. *Vicioideae.*—Leaves paripinnate, often terminating in tendrils. *Vicia* (Vetch), leaves with many leaflets; *Lathyrus* (Vetchling), usually with only two leaflets; *Pisum* (Pea), etc.

7. *Phaseoloideae.*—Climbing plants; leaves usually imparipinnate, frequently ternate. *Physostigma*; *Phaseolus.*

Geographical Distribution.—The large family of the *Papilionaceae* is not exclusively confined to any zone. The steppes of Western Asia are especially rich in Papilionaceous plants, represented in particular by shrubby species of *Astragalus*, from which gum-tragacanth is obtained. The leaflets of the pinnate leaves of the Tragacanth shrubs eventually fall off from the main stalks, which remain attached to the stems, and resemble long thorns. The gum is produced by the disorganisation of the stem-parenchyma, and exudes as a viscous fluid when incisions are made in the stems (Fig. 606). The most important cultivated plants are—*Pisum sativum*, the Pea; *Phaseolus vulgaris*, the common Kidney or French Bean; *Vicia Faba*, the Broad Bean; *Ervum Lens*, the Lentil; *Dolichos Soya*, the Soja (Soy) Bean of Japan and China; *Indigofera* species, Indigo (Tropics).

FIG. 605.—*Glycyrrhiza glabra* (½ nat. size).—*OFFICINAL*. (After BERG and SCHMIDT.)

POISONOUS.—The seeds of the Laburnum, *Cytisus Laburnum* (Fig. 607), a

FIG. 606.—*Astragalus gummifer* ($\frac{1}{2}$ nat. size).—*OFFICINAL.* (After SCHUMANN and ARTHUR MEYER.)

FIG. 607.—*Cytisus Laburnum.* Flowering branch and young legumes ($\frac{3}{8}$ nat. size).—*POISONOUS.*

small tree indigenous to the Alps, sometimes cultivated in gardens. It is characterised by its ternate leaves, and by its racemes of large, yellow flowers and many-seeded legumes. The other species of the same genus, *C. alpinus*, *C. purpureus*, *C. Weldini*, *C. biflorus*, have also toxic properties. *Coronilla varia* (Fig. 604), an herbaceous plant with umbels of rose-coloured flowers, is also considered poisonous, and the familiar ornamental climber, *Wistaria sinensis*.

FIG. 608.—*Myroxylon Pereirae* ($\frac{1}{2}$ nat. size).—*OFFICINAL*. (After SCHUMANN and A. MEYER.)

OFFICINAL.—*Astragalus* species, from which TRAGACANTHA is obtained. The stolons of *Glycyrrhiza glabra*, an herbaceous perennial of Southern Europe, constitute Liquorice Root, RAD. LIQUIRITIAE. From *Melilotus officinalis* is obtained HERBA MELILOTI ; from *Trigonella Foenum graecum*, SEMEN FOENUGRAECI ; from *Ononis spinosa*, RAD. ONONIDIS ; SPARTEINUM from *Spartium scoparium ;* from the seeds (Calabar beans) of *Physostigma venenosum*, a climbing plant of Western

Africa, is derived the alkaloid PHYSOSTIGMINUM. The stems of *Andira Araroba*, a tree native of Brazil, contain CHRYSAROBINUM in the form of a powdery excretion. The heart-wood of *Pterocarpus santalinus*, an East Indian tree, yields Red Sandalwood, LIGNUM SANTALI RUBRUM. The dried sap of *Pterocarpus marsupium* (East Indies) provides KINO. *Myroxylon toluifera* (= *Toluifera Balsamum*), a tree growing in South America, has cortical balsam-canals which yield the Balsam of Tolu, BALSAMUM TOLUTANUM; BALSAMUM PERUVIANUM, the Balsam of Peru, is supplied by *M. Pereirae* (= *Toluifera Pereirae*) (San Salvador) (Fig. 608).

Order 21. Myrtiflorae

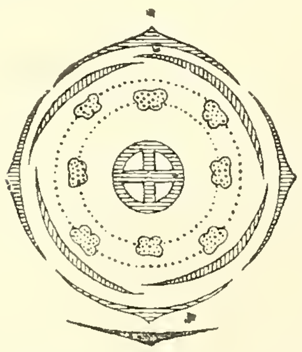


FIG. 609.—Floral diagram of *Oenothera* (*Onagraceae*).

Flowers PERIGYNOUS or EPIGYNOUS, usually ACTINOMORPHIC; perianth mostly TETRAMEROUS; andrœcium variable; gynœcium ENTIRELY SYNCARPOUS; ovary septated; seeds devoid of albumen. Leaves generally OPPOSITE and EXSTIPULATE.

The flowers of the *Myrtiflorae* are very similar to those of the *Rosiflorae*. Both orders are characterised by the variability displayed in the structure of their flowers. In both orders the flowers are actinomorphic, perigynous or epigynous, and have a tendency to increase the number of their parts by splitting, particularly in the andrœcium, which in consequence becomes polyandrous in the majority of the *Myrtiflorae*, just as in *Rosiflorae*. The main difference in the structure of the flowers of the two orders is exhibited in the gynœcium, which in the *Rosiflorae* consists, at least in the stigmatic region, of free carpels, while in the *Myrtiflorae*, with the exception of the group *Haloragidaceae*, the union of the carpels is complete, extending also to the style.

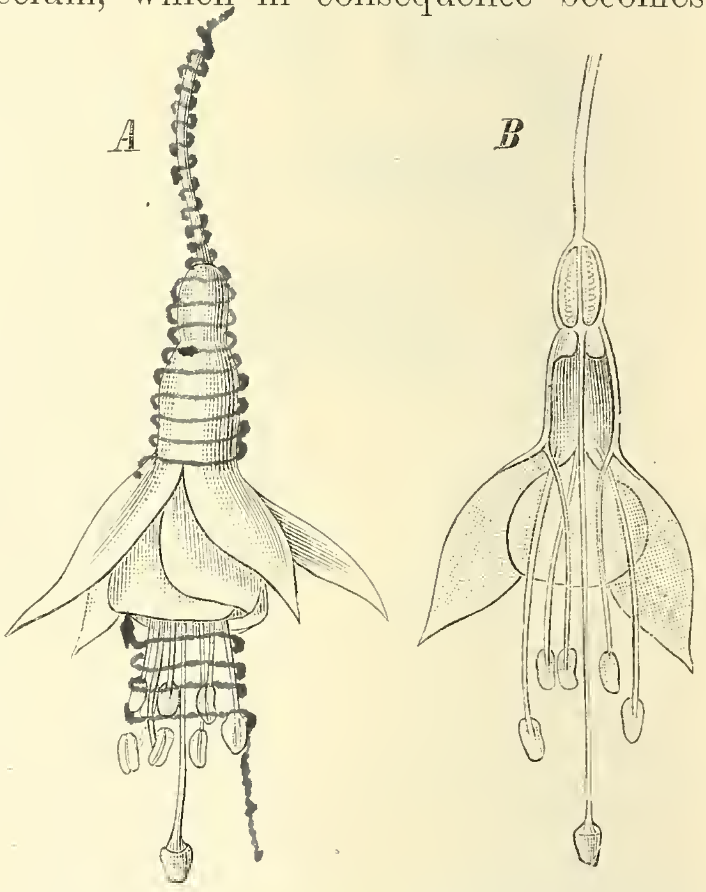


FIG. 610.—*Fuchsia globosa*. Flowers (nat. size).

The vegetative organs of this order in no wise resemble those of the *Rosiflorae*. The *Myrtiflorae*, on the contrary, have usually opposite, entire leaves, never compound; the leaves also are either exstipulate, or the stipules are small and fugacious. In this order, unlike the

Rosiflorae, many of the plants possess internal glands, which secrete ethereal oils.

Family **Onagraceae.**—Flowers EPIGYNOUS, actinomorphic, TETRAMEROUS THROUGHOUT; stamens OBDIPLOSTEMONOUS (Figs. 609, 610).

The *Onagraceae* include only herbs and shrubs. Their flowers are usually large and conspicuous, having often an elongated, tubular receptacle. Their fruit is many-seeded, and may be either dry or juicy.

REPRESENTATIVE GENERA. — *Epilobium* (Willow-herb) has a capsular fruit with hairy seeds; *Circaea* (Enchanter's Nightshade), with two-ranked leaves, fruit a nut; *Trapa* (Hornnut); *Oenothera* (Evening Primrose); *Fuchsia* (Fig. 610), with corollaceous calyx and tubular receptacle, cultivated. These are chiefly represented in Northern Europe by the red-flowered species of *Epilobium*, which grow in damp places and

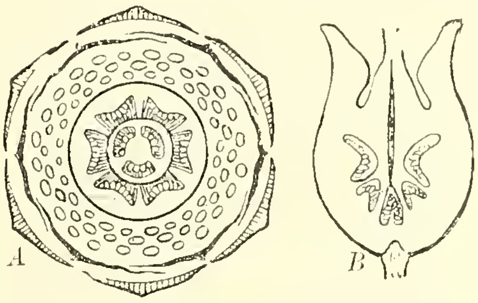


FIG. 611.—*A*, Floral diagram of *Punica granatum*. *B*, Longitudinal section of the ovary of the same plant. (After EICHLER.)

FIG. 612.—*Punica granatum* (½ nat. size).—*OFFICINAL*. (After BERG and SCHMIDT.)

on river-banks ; and by two large yellow-flowered species of *Oenothera* from North America.

Geographical Distribution. — The *Onagraceae* are native chiefly of the temperate zones of North and South America.

Family **Lythraceae.**—Flower hexamerous, perigynous, *Lythrum.*

Family **Haloragidaceae.**—Water plants with small, simply constructed flowers, *Myriophyllum, Hippuris.*

Family **Punicaceae.**—Comprising only the genus *Punica*, with two species.

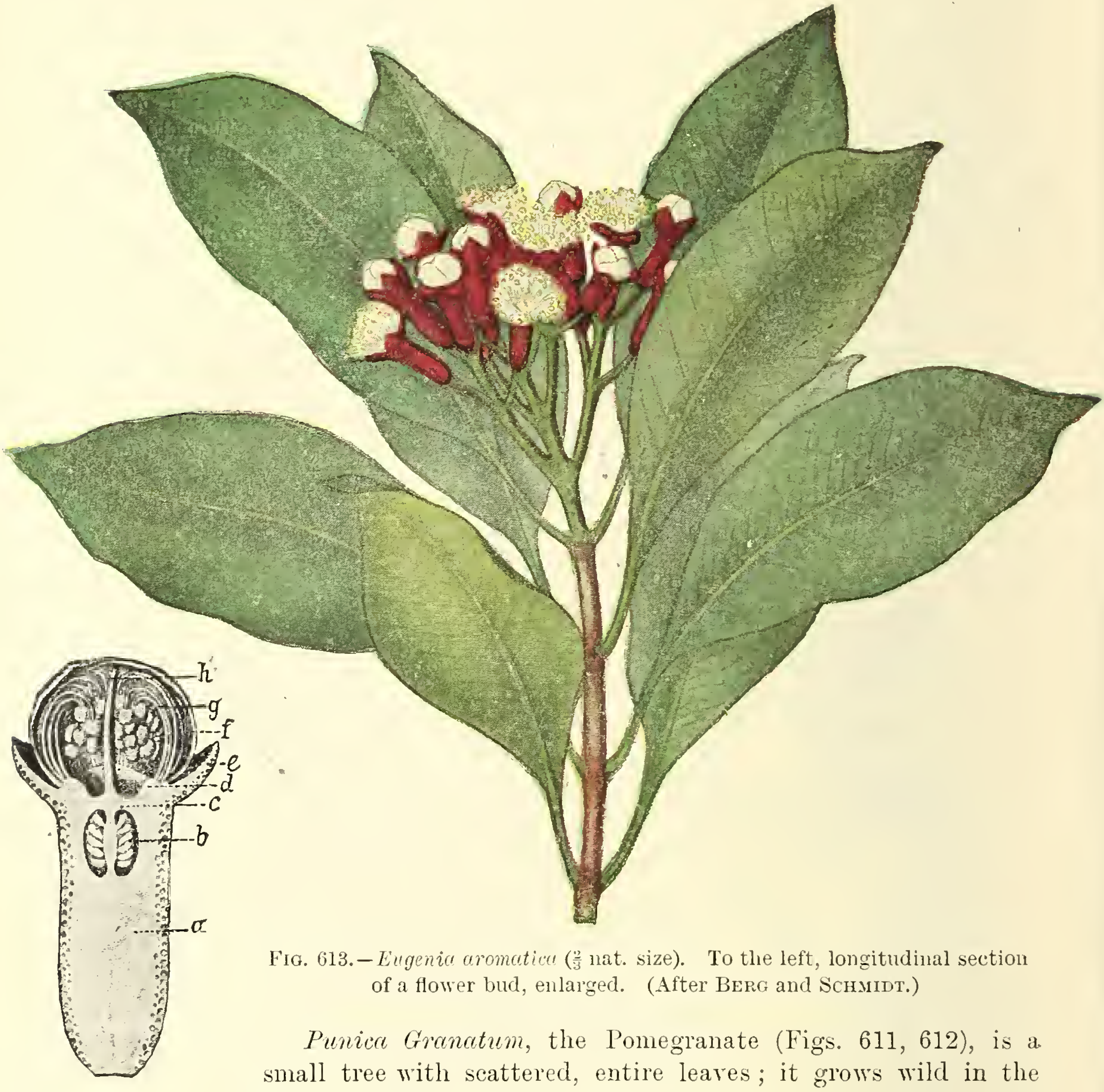


Fig. 613.—*Eugenia aromatica* (⅔ nat. size). To the left, longitudinal section of a flower bud, enlarged. (After Berg and Schmidt.)

Punica Granatum, the Pomegranate (Figs. 611, 612), is a small tree with scattered, entire leaves ; it grows wild in the East, but is frequently cultivated in Southern Europe. The flowers are epigynous ; they have fleshy, red receptacles, five to eight, also red and fleshy sepals, and an equal number of bright red petals, which are crumpled in the bud ; numerous stamens ; numerous united carpels disposed in two whorls. The fruit is a berry ; it retains the persistent calyx, and is filled with numerous seeds, whose succulent testa represents the edible portion of the fruit.

Officinal.—*Punica Granatum*, from which is obtained Cortex Granati.

Family **Myrtaceae.**—Flowers epigynous, actinomorphic, with four-to five-merous perianth and usually NUMEROUS stamens. Evergreen woody plants containing ETHEREAL OILS (Figs. 613, 614).

The plants comprised in this family are shrubs or trees, which are provided in all their organs with roundish glands containing ethereal oils, which give them an aromatic odour. The possession of ethereal oils is the most distinctive characteristic of the family. The leaves are opposite, entire, and of an elliptical shape. The flowers, which always have both a calyx and corolla, are solitary or clustered, and often very conspicuous. The corolla is usually white; it is sometimes reduced, and its function as an organ of attraction is assumed by the andrœcium, which acquires for this purpose a bright, usually red colour. Some species have haplostemonous or obdiplostemonous andrœcia; from such species, as is apparent from the transitional forms, those with polyandrous andrœcia have been developed by the division of the stamen-rudiments. The fruit is succulent or capsular, rarely nut-like.

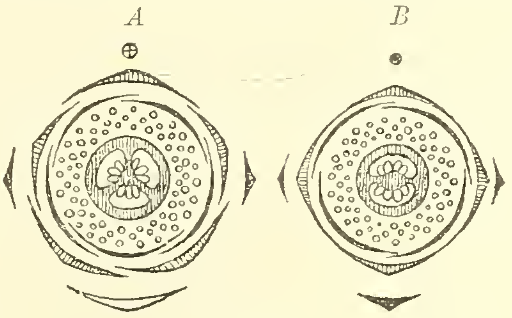


FIG. 614.—Floral diagrams of *Myrtaceae*. *A*, *Myrtus communis*; *B*, *Eugenia aromatica*. (After EICHLER.)

The *Myrtaceae* are confined to warmer countries. Europe possesses the single species *Myrtus communis*, the Myrtle. This family is especially characteristic of the Flora of Australia, in which it forms the most striking feature as regards the number of species and individuals, including, in particular, the Eucalyptus tree, which often attains a greater size than even the giant Conifers of California. Of late years Eucalyptus trees have been largely planted in all warm, malarial countries. Many produce delicious fruit, *e.g.* Guava, *Psidium Guava*. From other species spices are obtained. Cloves are the flower-buds of *Eugenia*, a small tree indigenous to the Moluccas, but cultivated in most tropical countries (Fig. 613); the stalk of the clove corresponds to the receptacle of the flower. The fruit of another tree of the same genus, *E. Pimenta*, is known as allspice.

OFFICINAL.—CARYOPHYLLI (Cloves) and OLEUM CAROPHYLLORUM from *Eugenia aromatica*; FOLIUM EUCALYPTI from *Eucalyptus globulus* (Australia, cultivated in Southern Europe); OLEUM CAJUPUTI from *Melaleuca leucadodendron* (Australia, Tropical Asia).

Order 22. Hysterophyta

This group, which is merely provisionally established, includes chiefly plants that are PARASITIC. Flowers epigynous, with simple or double perigone.

Family **Aristolochiaceae.**—Flowers actinomorphic or more frequently ZYGOMORPHIC; with simple corollaceous perigone consisting of three coherent members; andrœcium usually of six or twelve stamens, which are either free or united to the style (gynostemium); ovary four- to six-locular; fruit a capsule. Herbs and lianes NOT PARASITIC (Fig. 615).

This family comprises chiefly tropical plants with cordate or reniform leaves, represented in Europe and North America by the genera *Asarum* (*A. europaeum*) (Fig. 615) and *Aristolochia* (*A. clematitis*). *Aristolochia sipho*, the Pipe-Vine of North America, is a frequently cultivated climber.

The two families, **Rafflesiaceae** and **Balanophoraceae**, are leafless, often Fungus-like, root parasites entirely devoid of chlorophyll. The first-named family has solitary flowers, often of an enormous size. The flowers of *Rafflesia Arnoldi* (Sumatra) are the largest of all flowers, attaining a diameter of 1 metre. Both families are almost exclusively confined to the Tropics.

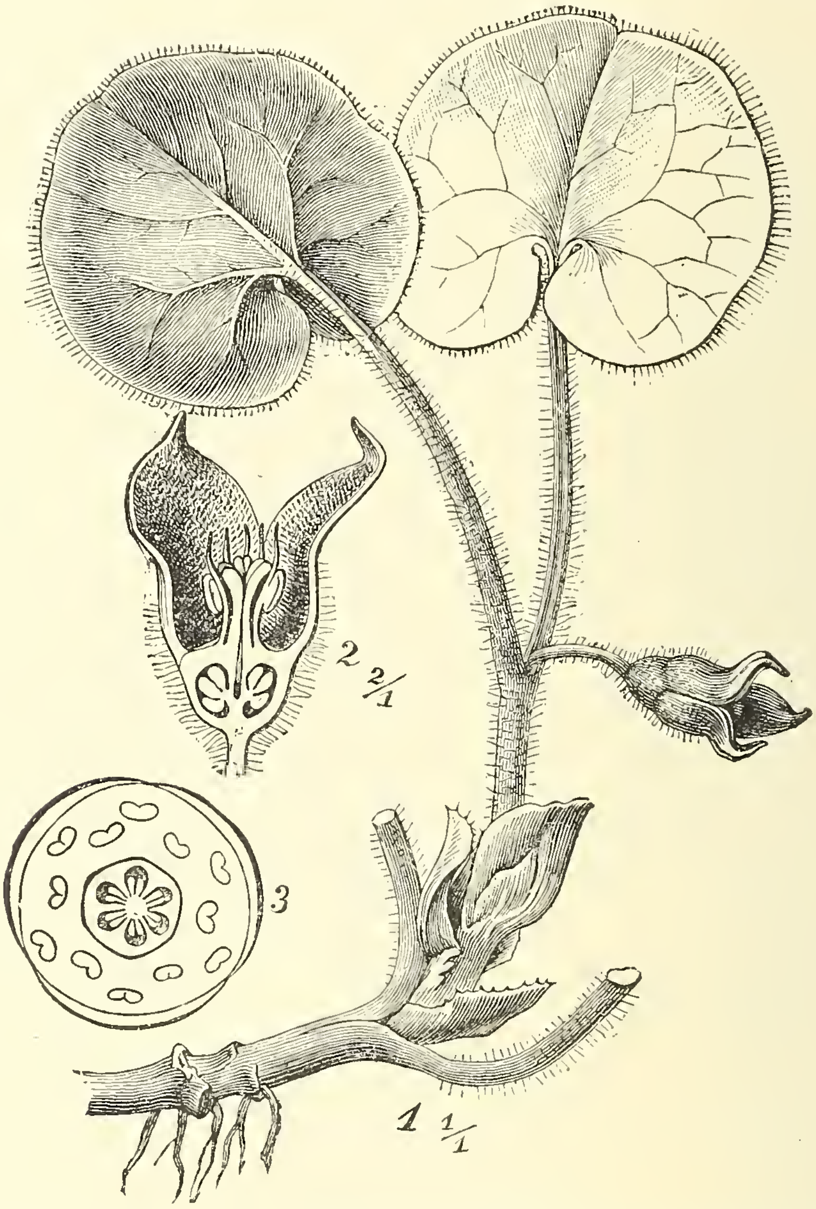


Fig. 615.—*Asarum europaeum.* 1, Flowering shoot; 2, flower cut through longitudinally; 3, floral diagram. (After Wossidlo.)

Family **Santalaceae**.—Parasitic plants with green leaves. Mainly tropical. *Thesium* in Europe.

Officinal.—*Santalum album*, a parasitic tree growing in East India, yields the valuable scented Sandal-wood, from which oil of sandal-wood, Oleum Santali, is obtained by distillation.

Family **Loranthaceae** (34).—Leafy shrubs parasitic on trees (Fig. 616).

The plants of this family are mostly tropical. *Loranthus europaeus* occurs upon Oaks in Eastern Europe. *Viscum album*, the European Mistletoe, is a small evergreen, dichotomously branching shrub, parasitic upon various species of trees. It absorbs its nourishment by means of haustoria consisting of root-like strands concealed between the cortex and wood of the host-branch. The flowers, which open in spring, have a tetramerous green perigone, to which the poricidal anthers are adherent. In the female flower any differentiation between placenta and ovules is wanting. The white berries produced by the female plants are eaten by birds,

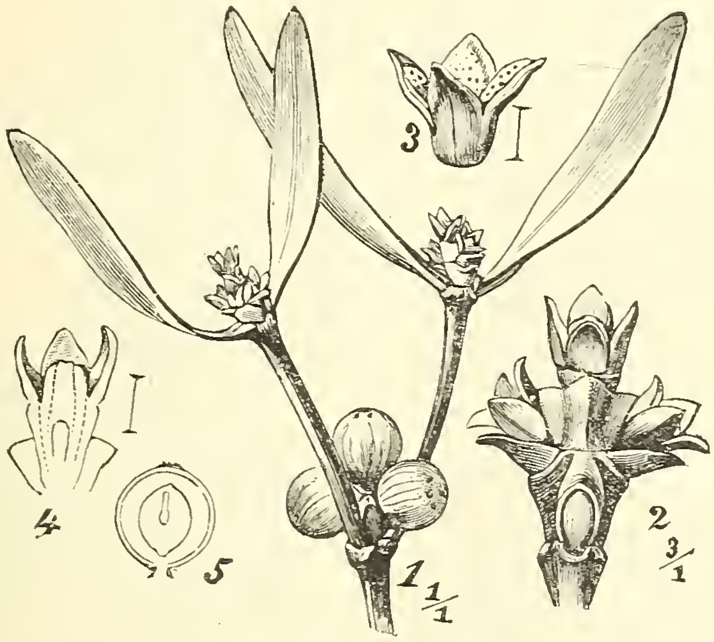


Fig. 616.—*Viscum album.* 1, Part of shoot with female flowers and fruit; 2, group of flowers; 3, a male flower; 4, female flower cut through longitudinally; 5, longitudinal section of fruit.—*Poisonous.* (After Wossidlo.)

which in freeing their bills of the sticky endocarp, by wiping them on the bark of trees, are at the same time instrumental in distributing the seeds.

Poisonous.—The berries of *Viscum album* when eaten by children have been known to produce symptoms of poisoning.

Group 2. Sympetalae

Perianth consisting of a calyx and an almost always SYMPETALOUS COROLLA.

The flowers are always cyclic, and in the majority of cases constructed, actually or theoretically, according to the formula K5, C(5), A5, G(2). THE STAMENS ARE GENERALLY INSERTED ON THE COROLLA. The fact that the gynœcium consists typically of only two carpels, must be regarded as the result of reduction, as flowers with five carpels sometimes occur.

Order 1. Ericinae

Flowers usually hypogynous, actinomorphic; formula, Kn, Cn, A2n, G(n), in which n is usually 5; corolla sometimes choripetalous; andrœcium OBDIPLOSTEMONOUS, NOT ADNATE TO THE COROLLA; pollen usually in tetrads; ovary MULTILOCULAR. Leaves needle-shaped or lanceolate.

Of all the *Sympetalae* the *Ericinae* approach most closely the

Choripetalae, not infrequently having free petals, while the stamens are inserted directly on the receptacle. They form a very natural group, whose close affinity is exhibited, not only in the structure of the flowers, but also in the vegetative organs. The axes are nearly always woody, usually comparatively short, and branching profusely close to the ground. The leaves are generally small and entire, in most cases leathery and evergreen. The flowers are always adapted to insect-pollination; they are often quite small, but in that case are aggregated in conspicuous racemes, usually of a white or crimson colour. The seeds are small.

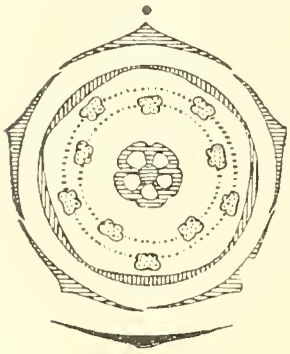


Fig. 617.—Floral diagram of *Vaccinium* (*Ericaceae*).

Family **Ericaceae.**—Flowers hypogynous or epigynous; corolla usually SYMPETALOUS; stamens free; anthers opening by pores or short slits; ovary WITH COMPLETELY SEPARATED LOCULI; placentæ not greatly thickened. Seeds with SEGMENTED embryo (Figs. 617, 618).

The anthers of many plants of this family have horn-like appendages (Fig. 618); the whole order is therefore sometimes inappropriately named *Bicornes*. At their upper extremities the thecæ are usually free and divergent. The pollen-grains cohere in tetrads. The fruit is a capsule, berry, or drupe, containing very small seeds with abundant endosperm. As regards the vegetative parts, the *Ericaceae* are typical of the order.

SUB-FAMILIES.—(1) *Rhododendroideae.* Flowers hypogynous; corolla fugacious; anthers without appendages; septicidal capsules. *Ledum, Rhododendron, Azalea,* etc. (2) *Arbutoideae.* Flowers hypogynous; corolla fugacious; anthers mostly appendiculate; loculicidal capsules or succulent fruits. *Andromeda, Arctostaphylos,* etc. (3) *Ericoideae.* Flowers hypogynous; corolla persistent; anthers mostly appendiculate; fruit a capsule. *Calluna*, calyx longer than the corolla; capsules

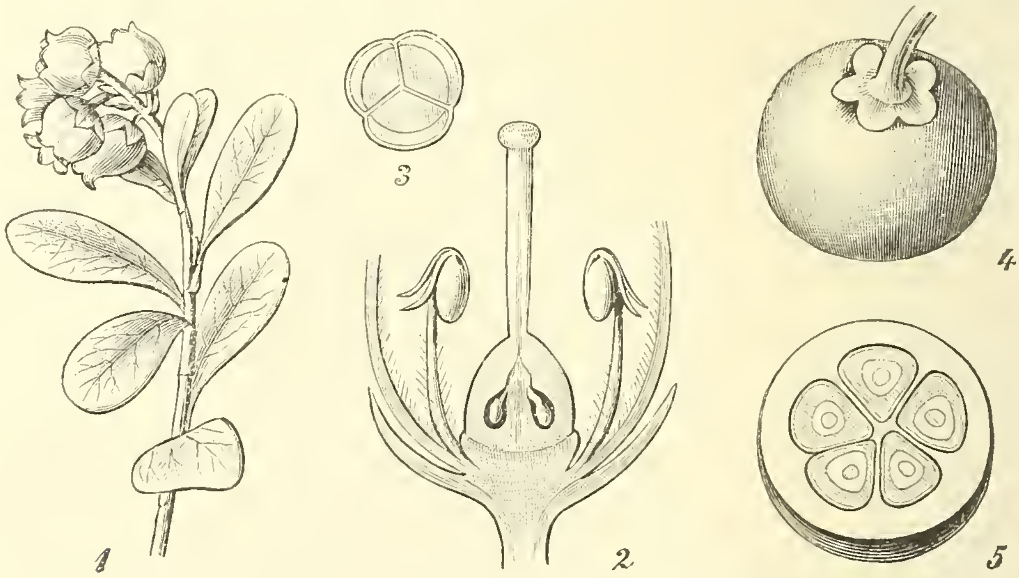


Fig. 618.—*Arctostaphylos Uva ursi.* 1, Flowering branch; 2, flowers in longitudinal section; 3, pollen-grains; 4, fruit; 5, fruit in transverse section.—*OFFICINAL.* (After BERG and SCHMIDT.)

septicidal. *Erica*, calyx shorter than the corolla ; capsules loculicidal. (4) *Vaccinioideae.* Flowers epigynous ; fruit a berry. *Vaccinium*, etc.

Geographical Distribution.—The plants included in this family are found widely distributed over the whole earth. Species of *Ericoideae* known as Heather, *Calluna vulgaris*, and different species of *Erica*, cover wide stretches of dry ground (heaths) in Central and Western Europe.

Fig. 619.—*Palaquium Gutta* ($\frac{1}{2}$ nat. size).—*Officinal.* (After Schumann and A. Meyer.)

The various species of *Erica*, frequently cultivated as pot-plants, are mostly from Southern Africa, where this genus is very largely represented and exhibits a wonderful richness of colour.

Poisonous.—The species of *Rhododendron* and *Azalea* contain toxic principles in all their organs. The incautious use of *Ledum palustre* (Herba Rosmarini silvestris) has often had fatal consequences. It is a small shrub with umbels of white flowers and linear leaves covered on the under side with rusty brown hairs.

Officinal.—*Arctostaphylos Uva ursi*, the Bearberry (Fig. 618), a small evergreen shrub with bright red campanulate flowers and small red drupes, yields Folia Uvae Ursi. *Vaccinium myrtillus* yields Fructus myrtilli.

Family **Pyrolaceae.**—As in the preceding family, except that the placentæ are very fleshy and the embryo not segmented. Humus plants with or without chlorophyll: *e.g. Pyrola* (Winter-green), evergreen perennials with racemes of white flowers; *Monotropa hypopitys.*

Order 2. Diospyrinae

Family **Sapotaceae.**—Tropical trees with latex in secretory cells. Officinal.—Gutta-percha, the dried latex of species of *Palaquium* (Malay Archipelago) (Fig. 619) and *Payena.*

Family **Styracaceae.**—The origin of Benzoinum, a resin procured by making incisions in the bark of *Styrax Benzoin*, from this plant has of late been questioned.

Order 3. Primulinae

Flowers hypogynous, actinomorphic, K5, C5, A5, G(5); andrœcium adnate to the corolla, epipetalous; ovary unilocular, with free central placentation.

The *Primulinae* exhibit the greatest diversity in their vegetative structure. Constant characters appear only in the flowers, which, however differently shaped and grouped, always have an epipetalous andrœcium and a unilocular ovary with a central placenta. Of all the other *Sympetalae*, the *Utriculariaceae* alone have similar placentæ.

Family **Primulaceae.**—Calyx herbaceous; style simple; ovules numerous; fruit a capsule (Figs. 620-622).

The plants of this family are for the most part small herbs. The flowers are sometimes small and inconspicuous, sometimes large and beautifully coloured; they are either solitary or grouped in inflorescences. The capsules split at the apex into valves, or the whole top falls off like a lid.

Representative Genera.—*Primula* (Primrose, Cowslip), with rosette of radical leaves, and flowers in umbels; corolla with long tube; capsule opening by valves. *Androsace*, like the preceding, except that the corolla has a shorter tube. *Lysimachia* (Loose-strife, Moneywort), stems with well-developed internodes and leaves. *Anagallis* (Pimpernel), fruit a pyxidium.

Geographical Distribution. — Most of the members of this family are indigenous to the Temperate and Arctic Zones of the Northern Hemisphere. Various species of *Primula* (*P. acaulis, auricula, sinensis*, etc.) and *Cyclamen*, etc., are cultivated as ornamental plants.

Poisonous.—The tubers of *Cyclamen europaeum*, the Alpine Violet, which occurs wild in Bavaria, are harmless and edible when cooked. *Anagallis arvensis* (Poor-man's weather-glass) and *A. coerulea* are slightly toxic. The glandular hairs of

FIG. 620.—*Cyclamen europaeum.* *A*, entire plant; *B*, fruit.—POISONOUS. (After REICHENBACH.)

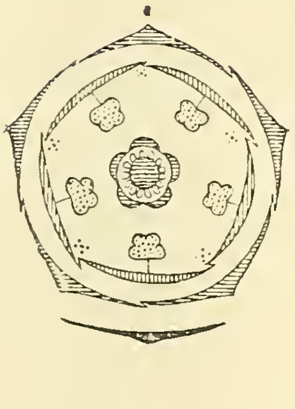


FIG. 621.—*Primulaceae.* Floral diagram (*Primula*).

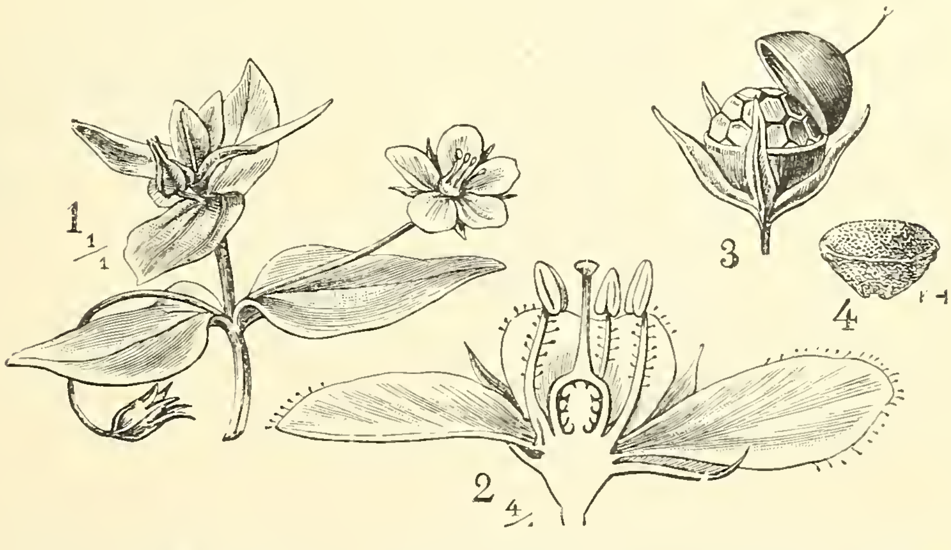


FIG. 622.—*Anagallis arvensis.* 1, Flowering branch; 2, a flower cut through longitudinally, showing the central placenta; 3, capsule; 4, seed.—*POISONOUS.* (After WOSSIDLO.)

Primula obconica and *P. sinensis* may give rise to inflammation of the skin or conjunctiva.

Family **Plumbaginaceae.**—Flowers with dry and membranaceous calyx, divided style, and one ovule. Fruit a capsule. Herbs. The dry calyx is usually brightly coloured ; the small flowers are aggregated into conspicuous inflorescences. Mainly halophytes. *Statice*, *Armeria* (Fig. 623).

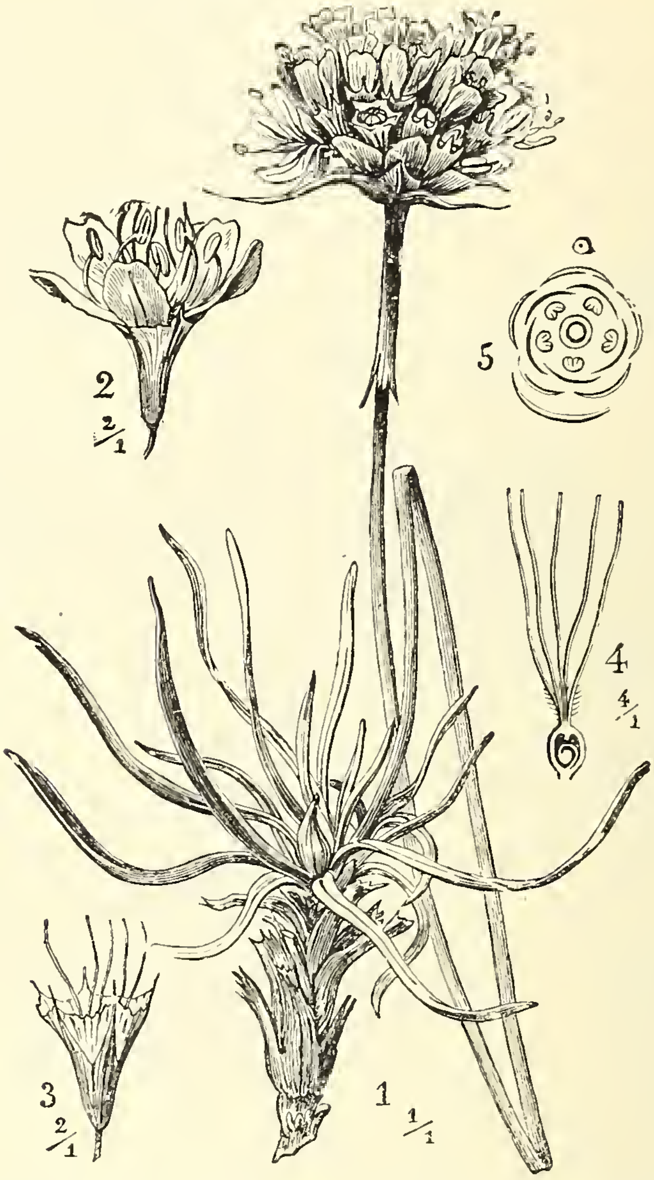


Fig. 623.—*Armeria vulgaris.* 1, Flowering plant ; 2, a flower ; 3, calyx with the projecting styles ; 4, gynœcium with ovary cut through longitudinally, showing the single ovule ; 5, floral diagram. (After Wossidlo.)

Order 4. Contortae

Flowers hypogynous, actinomorphic, with the formula Kn, Cn, An, $\underline{G2}$, in which n = 4 or 5 ; corolla frequently WITH CONTORTED ÆSTIVATION ; andrœcium adnate to the corolla. Leaves OPPOSITE, ENTIRE.

The *Contortae* constitute a heterogeneous order of plants, which may be most readily distinguished from other *Sympetalae* with actinomorphic flowers by their opposite, entire leaves. The contorted æstivation of the corolla, to which the name of the order has reference, although of frequent occurrence, is not a characteristic common to all the members of the order, nor is it restricted to the *Contortae.*

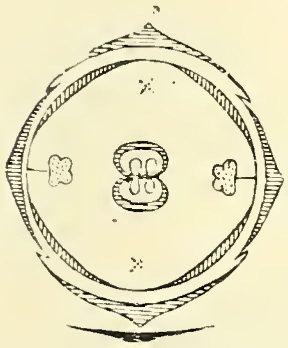


Fig. 624.—*Oleaceae.* Floral diagram (*Syringa*).

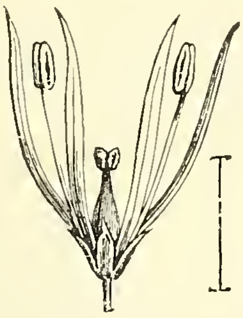


Fig. 625.—Flower of *Fraxinus Ornus.*—*OFFICINAL.* (After Wossidlo.)

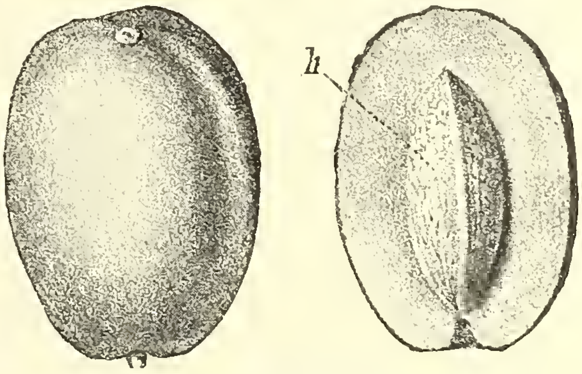


Fig. 626.—*Olea europaea.* Drupe.

Family **Oleaceae.**—Corolla with IMBRICATE or VALVATE æstivation; andrœcium of TWO stamens; gynœcium SYNCARPOUS; ovary

Fig. 627.—*Fraxinus Ornus* ($\frac{1}{2}$ nat. size).—*OFFICINAL.* (After Berg and Schmidt.)

BILOCULAR. Woody plants without latex; leaves exstipulate (Figs. 624-628).

The plants comprised in this family are either shrubs or trees. The leaves are usually simple and entire, more rarely lobed or compound. The flowers are generally small and in paniculate inflorescences; they have a small calyx and sometimes a synpetalous, sometimes a choripetalous corolla; in a few species they are apetalous. The two stamens constitute the most easily recognised characteristic of the family. Each loculus of the ovary contains two ovules. The fruit is a capsule, a dry indehiscent fruit, a berry or a drupe. Many species contain mannite.

FIG. 628.—*Olea europaea* (nat. size).—*OFFICINAL*. (After BERG and SCHMIDT.)

Representative Genera.—*Fraxinus* (Ash), with pinnate leaves ; *Ligustrum* (Privet), *Olea* (Olive), *Syringa* (Lilac), *Jasminum* (Jessamine).

Geographical Distribution.—The family *Oleaceae* is chiefly represented in Asia. Several species are familiar as ornamental plants, *e.g.* the different species of Lilac (*Syringa vulgaris*, from South-Eastern Europe ; *S. chinensis*, *S. persica*), Jessamine (*Jasminum grandiflorum*, etc.), *Forsythia viridissima*, etc. The most important economic plant of the family is the Olive-tree, *Olea europaea* (Figs. 626, 628), often cultivated in Southern Europe. The oil is extracted from the pulp of the ripe fruit, and also, although to a less extent, from the seeds. The wood (Olive-wood) is used for a variety of purposes.

Fig. 629.—*Strychnos nux vomica* (nat. size).—Officinal. (After Berg and Schmidt.)

Officinal.—Oleum Olivae (*vide supra*) ; Manna, the dried sap of the Manna-Ash, *Fraxinus Ornus* (Mediterranean) (Fig. 627).

Family **Loganiaceae.**— Poisonous — Curare, used by the South American Indians for poisoning arrows, and also as a Malayan arrow poison, is prepared from the bark of several species of *Strychnos*. The seeds of *Strychnos nux vomica* (Figs. 629, 630) (*vide infra*) are extremely poisonous.

Officinal.—*Strychnos nux vomica*, an East Indian tree whose fruit resembles an orange, but has a hard rind and usually only one seed, yields Semen Strychni and Strychninum. *Gelsemium nitidum*, a small herb growing in the United States, gives Radix Gelsemii.

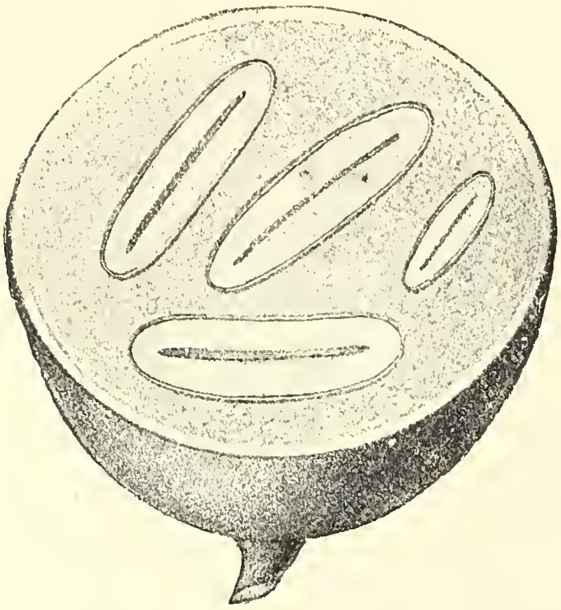


Fig. 630.—*Strychnos nux vomica.* Fruit cut across.

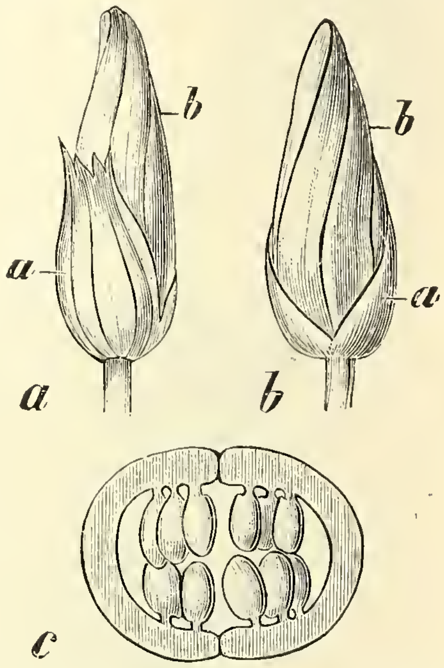


Fig. 631.—*Gentiana lutea.* *a* and *b*, Flower-buds (nat. size), showing calyx (*a*) and twisted corolla (*b*); *c*, transverse section of ovary.—*Officinal.* (After Berg and Schmidt.)

Fig. 632.—*Erythraea Centaurium.* 1, Apex of flowering shoot; 2, a flower cut through longitudinally; 3, anther; 4, fruit; 5, transverse section of fruit.—*Officinal.* (After Wossidlo.)

Family **Gentianaceae.**—Corolla with contorted æstivation; androecium haplostemonous; gynoecium syncarpous; ovary usually unilocular, with parietal placentæ. Herbs without latex, wholly restricted to the Temperate Zone (Figs. 631, 632).

The plants included in this family are large or small, glabrous herbs. Their leaves, which are almost always opposite and entire, are destitute of stipules. The flowers are often large and highly coloured, terminal and solitary, or more frequently they are arranged in dichasial inflorescences. The fruit is a two-valved, many-seeded capsule. Many species of *Gentianaceae* are rich in bitter principles.

REPRESENTATIVE GENERA.—*Gentiana* (Gentian), with straight anthers; *Erythraea* (Centaury), with anthers spirally twisted; *Chlora* (Yellow-wort); *Menyanthes* (Buckbean), with scattered, ternate leaves.

OFFICINAL.—*Gentiana lutea* and *G. pannonica, punctata, purpurea,* yield RADIX GENTIANAE; *Erythraea Centaurium,* HERBA CENTAURII; *Menyanthes trifoliata,* FOLIA TRIFOLII FIBRINI.

Family **Apocynaceae.**—Corolla with CONTORTED ÆSTIVATION; androecium haplostemonous; pollen granular or in tetrads; carpels usually FREE BELOW; RING-SHAPED STIGMA. Plants with LATEX (Figs. 633-635).

FIG. 633.—*Nerium Oleander* (reduced).—*POISONOUS.*

In this family are represented perennial herbs, shrubs, lianes, and trees; all usually evergreen, with opposite, entire leaves. The rotate or funnel-shaped flowers, which are often large and conspicuous, are aggregated in cymose inflorescences; the fruit is usually a capsule, both of whose free carpels (follicles) dehisce along the ventral suture, setting free numerous and often hairy seeds to be disseminated by the wind.

GEOGRAPHICAL DISTRIBUTION.—The *Apocynaceae* are chiefly indigeous to the Tropics, where numerous species are found. Familiar examples of this family are afforded by the Oleander, *Nerium Oleander*, and Periwinkle, *Vinca minor* (Fig. 634).

Poisonous.—*Nerium Oleander* (Fig. 633), an evergreen shrub of Southern Europe, with lanceolate leaves and large rose-coloured, more rarely white or light yellow, fragrant flowers. All parts of the Oleander are poisonous.

Officinal.—Various species of *Strophanthus* (*e.g. S. hispidus*), tropical lianes of Western Africa, yield Semen Strophanthi. Various tropical *Apocynaceae* (*e.g. Landolphia* sp. in Africa, *Hancornia* in Brazil, and *Willoughbeia* in the Malayan Archipelago) yield Caoutchouc. From *Aspidosperma Quebracho*, a tree native of the Argentine Republic, is derived Cortex Quebracho.

Fig. 634.—*Vinca minor*. 1, Apex of flowering shoot; 2, flower-bud cut through longitudinally; 3, a stamen; 4, pistil. (After Wossidlo.)

Family **Asclepiadaceae.**—Corolla with CONTORTED ÆSTIVATION; andrœcium haplostemonous; pollen-grains of each loculus of the anthers cohering together, in the form of a POLLINIUM; carpels with FREE OVARIES, united above into a PRISMATIC STIGMA. Plants with LATEX (Figs. 636, 637).

In their vegetative portions and fruit the *Asclepiadaceae* are like the *Apocynaceae*, but differ from them as from all other Dicotyledons in the structure of their andrœcia. The stamens are united, at least at the base; each of them bears a large dorsal appendage (Fig. 636, *A*). These staminal appendages together form a corona. Especially characteristic, also, are the club-shaped pollen-masses or pollinia, resembling those of the *Orchidaceae*. For the purpose of pollination by insects, the pollinia are attached in pairs (one pollinium from each pair of contiguous anthers) to a CORPUSCULUM or glandular outgrowth of the stigma (Fig. 636, *B*, *C*).

Fig. 635.—*Strophanthus hispidus* (½ nat. size).—*Officinal.* (After Schumann and A. Meyer.)

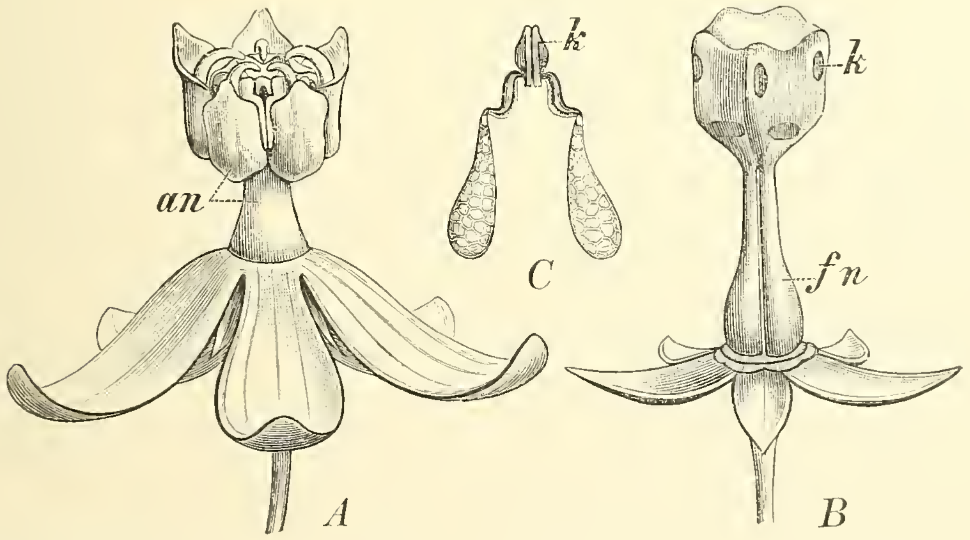


Fig. 636.—*Asclepias curassavica.* *A*, Flower ; *an*, andrœcium (× 4) ; *B*, calyx and gynœcium ; *fn*, ovary ; *k*, corpuscula (× 6) ; *C*, pollinia (magnified). (After Baillon.)

Geographical Distribution.—The *Asclepiadaceae* are chiefly native of the Tropics, where they are found as lianes or epiphytes. In the barren desert-regions of Southern Africa they are represented by leafless, Cactus-like succulents (*Stapelia*).

Poisonous.—The latex of most of the *Asclepiadaceae*, and also all parts of the species *Vincetoxicum officinale* (Fig. 637), possess toxic principles. The latter is a small, inconspicuous, white-flowered plant, with capsules and long-haired seeds.

Fig. 637.—*Vincetoxicum officinale* ($\frac{1}{2}$ nat. size).—*Poisonous.*

Fig. 638.—*Convolvulus arvensis.* 1, Part of a stem with flowers; 2, a flower cut through longitudinally; 3, fruit; 4, seed; 5, floral diagram. (After Wossidlo.)

Officinal.—The bark of *Gonolobus Condurango* and other lianes of Peru and Ecuador yield Cortex Condurango.

Order 5. Tubiflorae

Flowers hypogynous, ACTINOMORPHIC, sometimes slightly zygomorphic, generally with the formula K5, C5, A5, G$\underline{(2)}$; stamens COMPLETE IN NUMBER, inserted on the corolla; ovary bilocular (rarely trilocular), WITH TWO OVULES in each loculus; loculi frequently chambered by FALSE DISSEPIMENTS. Leaves ALTERNATE.

The *Tubiflorae* are a group consisting mostly of herbs. Their floral construction points clearly to the group being a natural one.

Family **Convolvulaceae.**—Corolla FOLDED LONGITUDINALLY in the bud, TWISTED, usually to the right; ovary bilocular, with two erect ovules in each loculus; loculi often two-chambered; embryo curved. Mostly CLIMBING herbs and shrubs, usually with LATEX (Fig. 638).

The majority of the plants in the family are sinistrorse herbaceous climbers, with heart-shaped leaves and conspicuous flowers, usually with a funnel-shaped, slightly lobed corolla. The fruit is a capsule or berry. In addition to the normally assimilating leafy species, the family of the *Convolvulaceae* includes a number of thread-like parasitic plants almost devoid of chlorophyll (*Cuscuta*). The species of this genus twine about other plants and obtain nourishment by sending out haustoria into their stems (cf. p. 208, Fig. 186).

REPRESENTATIVE GENERA.—*Convolvulus*, with two-cleft style (*e.g. C. arvensis*, Bindweed; *Calystegia* (Bracted Bindweed), like the preceding, but with two large bracteoles; *Ipomoea*, style four-cleft (*e.g. I. purpurea*, the common Morning Glory); *Cuscuta* (Dodder); *Ipomoea Batatas* is largely cultivated for the tuberous roots (Sweet Potatoes).

OFFICINAL.—*Ipomoea Purga*, a Mexican climbing plant, yielding TUBERA JALAPAE and RESINA JALAPAE; SCAMMONIUM, the latex from the root of *Convolvulus Scammonia* (Asia Minor).

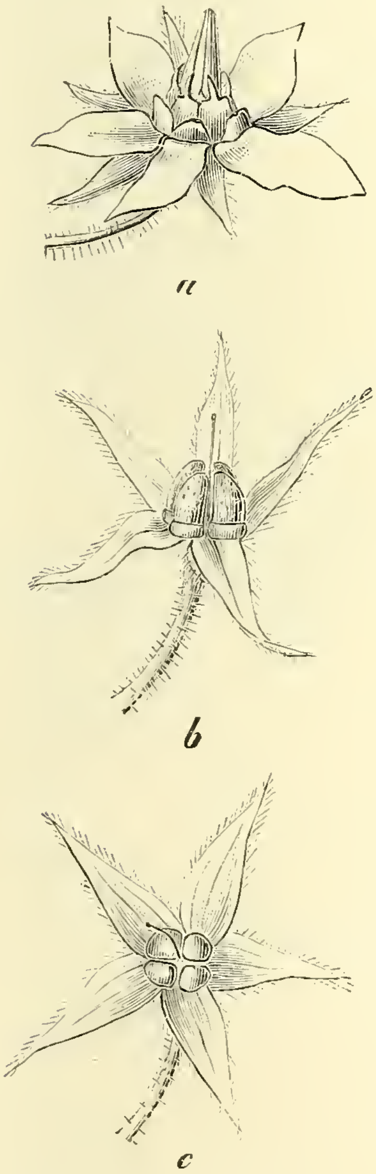


FIG. 639.—*Borago officinalis*. *a*, Flower; *b* and *c*, fruit (nat. size).

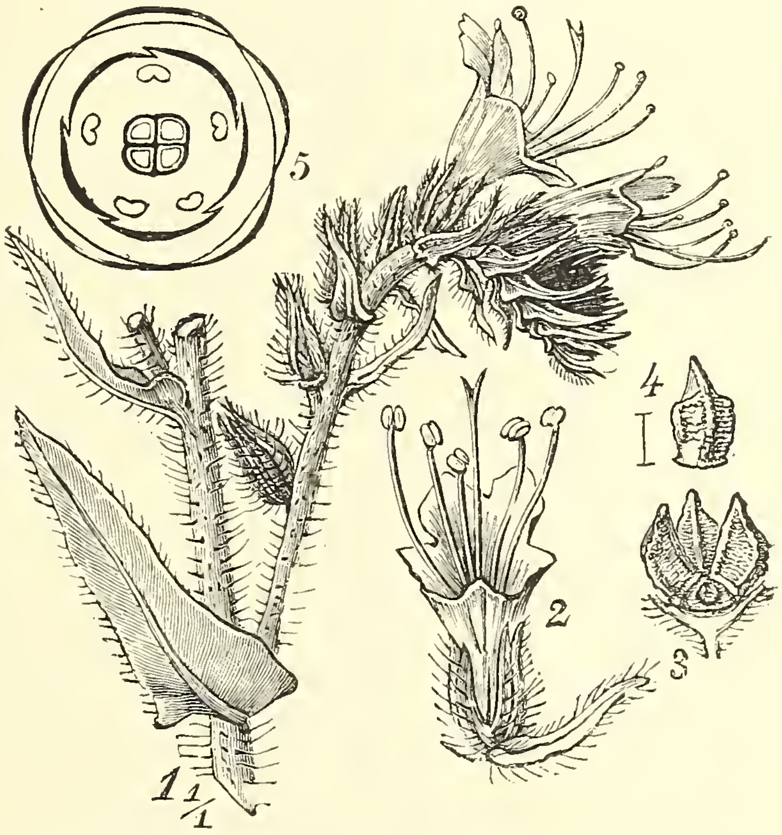


FIG. 640.—*Echium vulgare*. 1 Inflorescence; 2, a flower; 3, fruit; 4, a single nutlet; 5, floral diagram. (After WOSSIDLO.)

The **Polemoniaceae** differ from the *Convolvulaceae* in having three carpels and no latex. Various species of *Polemonium*, *Cobaea*, and *Phlox* are ornamental plants.

Family **Boraginaceae**.—Corolla with imbricate æstivation; ovary dimerous, but deeply FOUR-LOBED OR CHAMBERED, with one suspended ovule in each chamber. Style inserted in the depression between the four projecting lobes of the carpels. The fruit is a FOUR-PARTITE SCHIZO-

CARP, consisting of four nutlets. Seeds usually without endosperm. Inflorescences SCORPIOID (Figs. 639, 640).

The *Boraginaceae* are for the most part herbaceous plants, and constitute one of the most natural and easily recognisable families. The succulent stems, covered with harsh hairs, the entire leaves, the scorpioid inflorescences with spirally coiled branches, the usually blue flowers, and the distinctive structure of the fruit, all serve to give the plants comprised in this family a highly characteristic appearance.

REPRESENTATIVE GENERA.—(*a*) Throat of the corolla with scales: *Borago* (Borage), stamens with horn-like appendages; *Symphytum* (Comfrey); *Myosotis* (Forget-me-not). (*b*) Throat of corolla without scales: *Pulmonaria* (Lungwort); *Echium* (Viper's Bugloss), with zygomorphic flowers (Fig. 640); *Cerintha*, leaves glabrous, with waxy covering; *Lithospermum* (Gromwell), nutlets stony, owing to the presence of calcium carbonate. Anomalous: *Heliotropium* (Heliotrope), with undivided ovary prolonged into an apical style.

GEOGRAPHICAL DISTRIBUTION.—The members of this family abound in the North Temperate Zone, particularly in the Mediterranean countries.

To the *Tubiflorae* belong also the two families **Hydrophyllaceae** (chiefly indigenous to America) and **Cordiaceae** (tropical woody plants, with drupaceous fruit). These two families, neither of which is represented in Europe, stand in close relationship to the *Convolvulaceae* as well as to the *Boraginaceae*.

Order 6. Personatae

Flowers hypogynous, mostly ZYGOMORPHIC; typically with the formula K5, C5, A5, G$\underline{(2)}$, but usually with a REDUCED ANDRŒCIUM. Stamens inserted on the corolla; ovary dimerous, bilocular, rarely with false dissepiments, usually with NUMEROUS ovules. Leaves alternate or opposite.

Included in this order are herbs and woody plants, generally with conspicuous flowers. The corolla is commonly bilabiate. In most instances the andrœcium is reduced to four stamens, disposed in two pairs of unequal length; more rarely only two stamens are present. The fruit is most frequently a capsule.

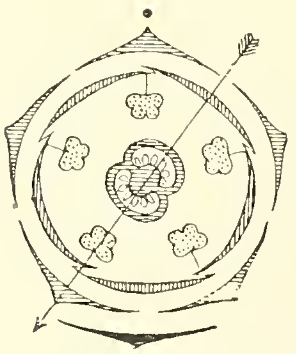


FIG. 641.—*Solanaceae*. Floral diagram (*Petunia*).

The *Solanaceae* are, phylogenetically, probably the oldest family of the order, and in their generally actinomorphic flowers and pentamerous andrœcia they exhibit a close affinity to the *Tubiflorae*, particularly to the *Hydrophyllaceae*, in which the gynœcia have a similar oblique position. The *Solanaceae* are also allied to the *Boraginaceae*, with which they are connected by the small family *Nolanaceae*. (Plaited corolla, seeds and unequally paired leaves, as in the *Solanaceae*; fruit a schizocarp, as in the *Boraginaceae*.) Between the *Solanaceae* and *Scrophulariaceae*, on the other hand, there are no uniformly constant distinctions. The other families embraced by the *Personatae*, with the exception of the *Acanthaceae*, *Globulariaceae*, and *Plantaginaceae*, are all closely allied to the *Scrophulariaceae*.

Family **Solanaceae.**—Corolla PLAITED in the bud, usually ACTINOMORPHIC; andrœcium PENTAMEROUS; carpels obliquely placed with reference to the median plane of the flower; seeds with endosperm (Figs. 641-647).

The majority of the *Solanaceae* are herbs (in the Tropics also represented by shrubs and small trees), with numerous, often glandular hairs, and not unfrequently with prickles. In the region of the inflorescence the leaves are often borne in pairs, consisting of one large and one smaller leaf. This peculiar disposition of the leaves is due to the displacement of the bracteoles and subtending bracts, which adhering to their growing axillary shoots are carried up a distance on them (Fig. 646). The flowers are either solitary or grouped in inflorescences; they are variously shaped and usually have a five-lobed corolla, often of a pale violet colour. The oblique position of the carpels (Fig. 641) is a distinctive characteristic of the flowers of this family. The fruit is a berry or capsule. The seeds are generally reniform, and contain a curved embryo embedded in an oily endosperm.

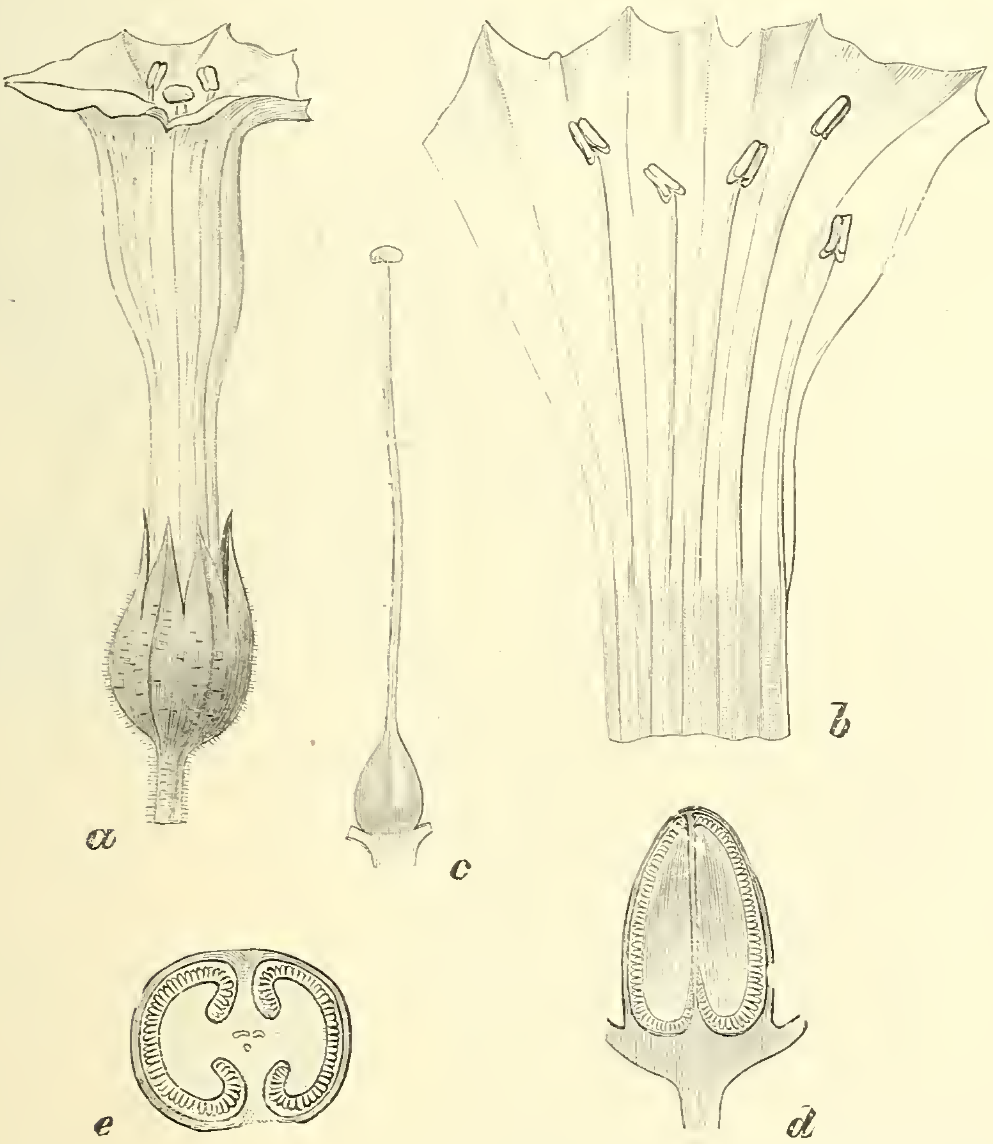


FIG. 642.—*Nicotiana Tabacum.* *a*, Flower; *b*, corolla, cut open and spread out flat; *c*, ovary: *d* and *e*, young fruit. (*a*, *d*, *c*, nat. size; *e*, *d*, ×2.)

Fig. 643.—*Solanum Dulcamara* ($\frac{1}{2}$ nat. size). — *Officinal*, *Poisonous*. (After Berg and Schmidt.)

Fig. 644.—*Nicotiana Tabacum* ($\frac{1}{2}$ nat. size).—*Poisonous* and *Officinal*.

REPRESENTATIVE GENERA.—(*a*) Fruit a capsule: *Nicotiana; Datura*, capsule four-valved; *Hyoscyamus*, flowers zygomorphic, capsule dehiscing transversely, a pyxidium. (*b*) Fruit a berry: *Solanum*, anthers converging, opening by pores; *Lycopersicum; Capsicum; Atropa; Mandragora; Physalis*, the baccate fruit enveloped by the persistent red calyx.

GEOGRAPHICAL DISTRIBUTION.—The *Solanaceae* comprise chiefly plants of the Tropical Zone. In addition to the officinal plants, this family contains a number of other economic plants, all of which are natives of South America: the Potato, *Solanum tuberosum;* the Tobacco-plant, *Nicotiana Tabacum* (Fig. 644), and *N. rustica;* the Tomato, *Lycopersicum esculentum*, etc. The Potato plant grows wild in the Andes mountains in Chili: it was first introduced into Spain and thence into Europe in the latter half of the sixteenth century. The first introduction of Tobacco into Europe occurred about the same time. It is stated that *Nicotiana Tabacum* is still found growing wild in Peru and Ecuador.

FIG. 645.—*Hyoscyamus niger* (½ nat. size).—*OFFICINAL, POISONOUS.* (After BERG and SCHMIDT.)

FIG. 646.—*Atropa Belladonna* (½ nat. size). *POISONOUS* and *OFFICINAL.*

POISONOUS.—Almost all of the plants of this family are wholly or in part poisonous, in most cases on account of the alkaloids they contain. All parts of *Solanum tuberosum* contain solanine; on that account it is dangerous to eat potatoes that have turned green or such as have developed shoots. *Solanum Dulcamara* (Bitter-sweet, Fig. 643) contains solanine in all its parts, with the exception of the harmless berries. Solanine occurs, on the other hand, in the black berries of *Solanum nigrum* (Common Nightshade), a weed frequently growing in fields. The unripe fruits of the Tomato have been known, when eaten, to produce symptoms of poisoning. *Atropa Belladonna*, the Deadly Nightshade (Fig. 646), is the most noxious plant of this group. It is an herbaceous plant with reddish brown campanulate flowers and very poisonous black berries enveloped by the persistent calyx. *Datura Stramonium*, the Thorn-Apple (Fig. 647), is also a narcotic, poisonous, herbaceous plant, of common occurrence on waste ground. It branches dichotomously and bears white, funnel-shaped flowers producing large prickly capsules. *Hyoscyamus niger*, Black Henbane (Fig. 645), grows in situations similar to those in which the Thorn-Apple is found; it also possesses dangerous narcotic properties. The flowers, which are disposed in one-sided inflorescences, have a funnel-shaped, five-lobed, yellow corolla marked with violet veins; the fruit is a pyxidium. *Nicotiana Tabacum* (Fig. 644) contains toxic principles in all its parts.

FIG. 647.—*Datura Stramonium*. *POISONOUS* and *OFFICINAL* (½ nat. size). (After BERG and SCHMIDT.)

OFFICINAL.—*Atropa Belladonna* yields FOLIA ET RADIX BELLADONNAE, ATROPINUM; *Datura Stramonium*, FOLIA STRAMONII, SEMEN STRAMONII; *Hyoscyamus niger*, HERBA HYOSCYAMI; *Capsicum annuum*, FRUCTUS CAPSICI; *Nicotiana Tabacum*, FOLIA NICOTIANAE; *Solanum Dulcamara*, CAULES DULCAMARAE; *Scopolia carniolica*, SCOPOLAMINUM.

FIG. 648.—*Digitalis purpurea* ($\frac{1}{2}$ nat. size). *POISONOUS* and *OFFICINAL*.

Family **Scrophulariaceae**.—Corolla most frequently ZYGOMORPHIC, NEVER PLAITED in the bud; andrœcium usually REDUCED to FOUR OR TWO STAMENS; carpels MEDIAN (Figs. 648-652).

Of the plants comprising the *Scrophulariaceae*, the majority are herbs with simple, toothed, rarely lobed leaves, which may be opposite or alternate but never unequally paired, as in the *Solanaceae*. Many species, although provided with leaves, are root-parasites. The flowers, whether solitary and axillary or in racemes, always have a lateral origin. In some genera, *Verbascum*, the flowers are nearly actinomorphic, with pentamerous andrœcium (Fig. 649, *A*, 651); but in most of the forms they are distinctly zygomorphic, while the andrœcia are also reduced. In cases where one stamen is rudimental (*Scrophularia*) or suppressed, it is usually the posterior one. Sometimes, in consequence of more extended suppression, only two stamens remain (*e.g. Gratiola*, Fig. 649, *B*). The fruit is a capsule, or less frequently a berry.

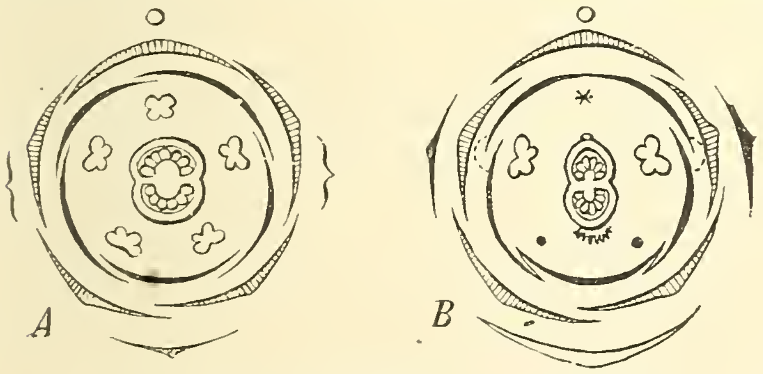


FIG. 649.—*Scrophulariaceae*. Floral diagrams. *A*, *Verbascum*; *B*, *Gratiola*. (After EICHLER.)

SUB-FAMILIES AND REPRESENTATIVE GENERA, *A*, Ovary bilocular.—(1) *Antirrhinoideae*. Corolla with descending æstivation (*i.e.* the two posterior petals overlap the lateral, which in turn enclose the anterior stamen); autotrophic plants. *Verbascum* (Mullein), with five fertile stamens; *Scrophularia* (Figwort); *Antirrhinum* (Snapdragon), corolla with short spur and two closed lips, capsule opening by pores; *Linaria* (Toad-Flax), corolla with long spur, otherwise as in the preceding genus; *Digitalis* (Foxglove) corolla obliquely campanulate, capsule opening by valves; *Gratiola* (Hedge-Hyssop); *Veronica* (Speedwell). (2) *Rhinanthoideae.* Corolla with ascending æstivation (*i.e.* the two posterior petals overlapped by the lateral); green plants, more rarely devoid of chlorophyll, parasitic by means of their haustoria on the roots of other plants. *Rhinanthus* (Yellow-Rattle); *Melampyrum* (Cow-Wheat); *Euphrasia* (Eyebright); *Pedicularis* (Lousewort). *B*, Ovary unilocular. (3) *Gesneroideae* (Fig. 652), *Gloxinia*, *Orobanche.* Parasites devoid of chlorophyll; several species in Europe.

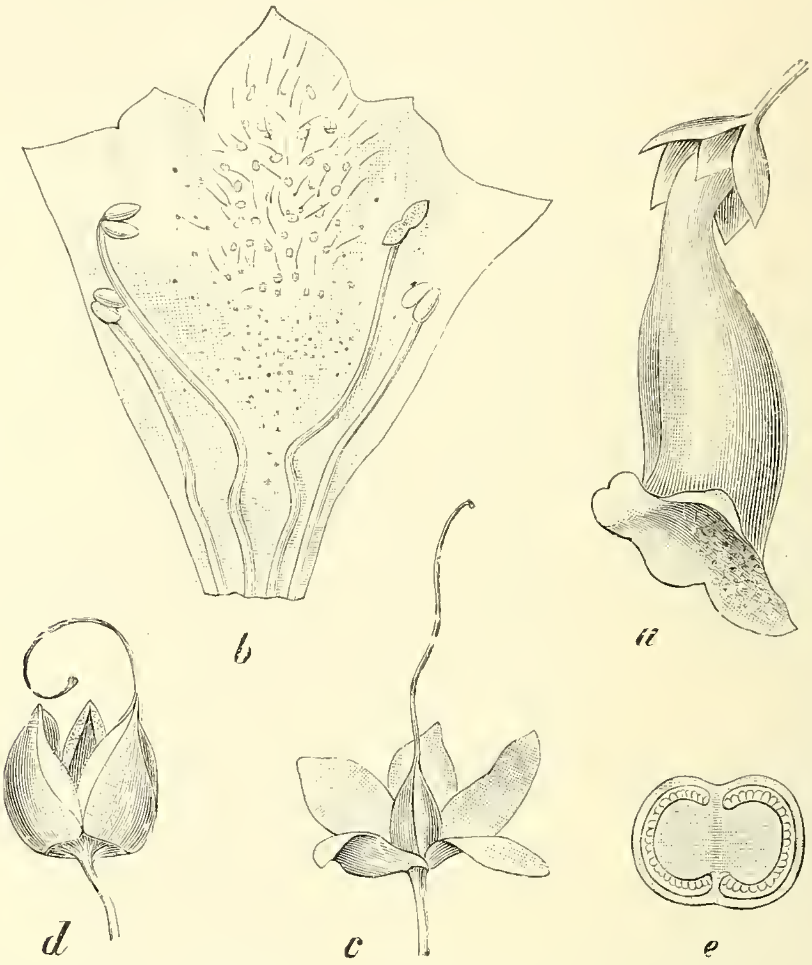


Fig. 650.—*Digitalis purpurea.* *a*, Flower; *b*, corolla cut open and spread out; *c*, calyx and pistil; *d*, fruit after dehiscence; *e*, transverse section of fruit (nat. size).

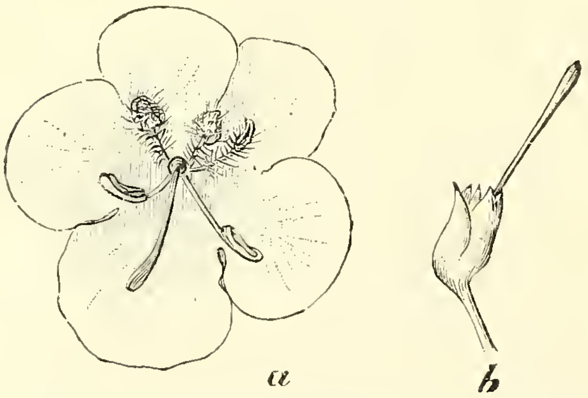


Fig. 651.—*Verbascum thapsiforme.* *a*, Flower; *b*, calyx and style (nat. size).—*Officinal.*

Geographical Distribution.—The *Scrophulariaceae* are of frequent occurrence in the temperate zones of both hemispheres, growing in the most varied situations. Many are ornamental plants, *e.g.* *Antirrhinum majus*, various species of *Veronica*, *Paulownia imperialis* (arborescent).

Poisonous.—*Digitalis purpurea* (Fig. 648), an unbranched, thickly-leaved, hairy biennial bearing terminal, one-sided racemes of reddish campanulate flowers; all parts exceedingly poisonous. *Gratiola officinalis*, a perennial, glabrous herb, growing in damp situations to a height of 30 cm., with narrow, toothed leaves and axillary tubular flowers, of a whitish colour. Two stamens and two staminodes.

OFFICINAL.—*Digitalis purpurea*, the Purple Foxglove (Figs. 648, 650) yields FOLIA DIGITALIS; *Verbascum thapsiforme* (Fig. 651) and *V. phlomoides*, FLORES VERBASCI.

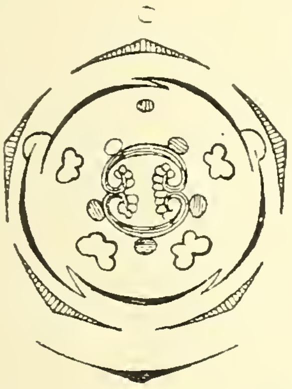


FIG. 652.—Floral diagram of *Gesnera pendulina* (*Gesneroideae*). (After EICHLER.)

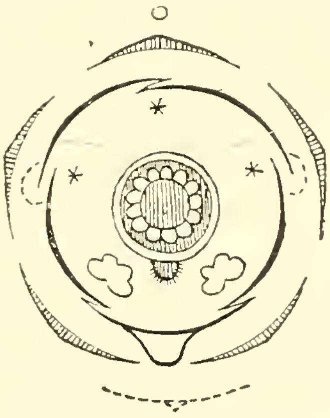


FIG. 653.—Floral diagram of *Pinguicula alpina* (*Utriculariaceae*). (After EICHLER.)

Family **Bignoniaceae**.—Mostly woody climbers, with winged seeds in a dry capsule. Mostly Tropical. *Catalpa bignonioides* and *Tecoma radicans*, both from North America, are cultivated. *Jacaranda* (South America) gives a timber.

FIG. 654.—*Plantago major*. 1, Entire plant; 2, flower with subtending bract; 3, fruit; 4, seed; 5, floral diagram. (After WOSSIDLO.)

Family **Utriculariaceae**. — Free central placentation. Insectivorous plants growing in marshy places, *Utricularia*, *Pinguicula* (Fig. 653).

Family **Plantaginaceae**. — Flowers small, actinomorphic, which, owing to suppression (calyx, andrœcium) and cohesion (corolla), have become apparently tetramerous. Mostly anemophilous (except *Plantago media*) herbs, *Plantago* (Fig. 654).

Order 7. Labiatiflorae

Flowers hypogynous, almost always zygomorphic, theoretically with the formula K5, C5, A5, G$(\underline{2})$, but usually with REDUCED ANDRŒCIA (A4 or A2); stamens inserted on the corolla; ovary bilocular, with FOUR erect ovules, each loculus SUBDIVIDED BY A FALSE DISSEPIMENT. Fruit commonly a schizocarp. Leaves generally opposite.

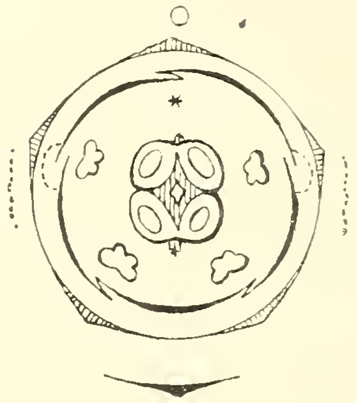


Fig. 655.—Floral diagram of *Verbena officinalis*. (After Eichler.)

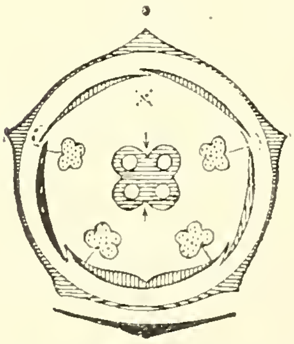


Fig. 656.—Floral diagram of *Lamium* (*Labiatae*).

Fig. 657.—*Mentha piperita* (½ nat. size).—*Officinal*. (After Berg and Schmidt.)

The plants constituting this order are herbs or shrubs, rarely trees; their vegetative organs are usually hairy and often aromatic. The flowers are axillary, in most instances distinctly zygomorphic and aggregated in inflorescences. The fruit is commonly a four-partite schizocarp, more rarely a drupe or capsule.

Family **Labiatae.**—Ovary DEEPLY FOUR-LOBED, bicarpellary, four-chambered, with GYNOBASIC style (attached to the base instead of to the summit of the ovary); fruit a FOUR-PARTITE SCHIZOCARP with four nutlets. Herbs and small shrubs with quadrangular stems and opposite leaves; inflorescences dichasial (Figs. 656-659).

FIG. 658.—*Melissa officinalis.*—OFFICINAL. (After BERG and SCHMIDT, ½ nat. size.)

The *Labiatae* constitute one of the most natural families of the vegetable kingdom. The quadrangular stems and decussate leaves give the plants of this family a distinctive character, which is enhanced by their odour and general hairiness. The aroma so characteristic of many species is due to the presence of an ethereal oil secreted by small glandular hairs scattered over the surface of the stems and leaves. Not less characteristic of this family is the apparent disposition of the short-stalked flowers in whorls, which in reality represent axillary scorpioid cymes, sometimes termed verticillasters. The separate inflorescences often become aggregated in terminal heads and spikes, as in the Thyme and Peppermint. The calyx (Fig. 659, *d*, *e*) is gamosepalous and five-toothed. The corolla is usually bilabiate, with two lobes in the upper lip and three in the under; it is variously coloured, but most frequently of a carmine or violet colour. The andrœcium chiefly resembles that of the *Scrophulariaceae*, while the gynœcium is constructed as in the *Boraginaceae*, consisting of an originally bilocular ovary whose carpels become deeply constricted longitudinally and thus subdivided, each into two chambers. The NUTLETS (Fig. 659, *d*, *e*) of the fruit always have a hard outer wall; they are sometimes partially aborted.

Representative Genera.—*Ajuga* (Bugle), with short upper lip; *Teucrium* (Germander), upper lip deeply cleft; *Stachys* (Betony, Hedge-Nettle), *Galeopsis* (Hemp-Nettle), and *Lamium* (Dead-Nettle), with helmet-shaped upper lip; *Nepeta* (Cat-Mint) and *Glechoma* (Ground-Ivy), unlike most of the other genera, with a long posterior stamen; *Mentha* (Mint), with almost actinomorphic corolla and stamens of about equal length; *Thymus* (Thyme); *Origanum* (Marjoram); *Lavandula* (Lavender); *Salvia* (Sage) and *Rosmarinus* (Rosemary), with two stamens, each of which has only a fertile half-anther.

Geographical Distribution.—Like most aromatic plants, the *Labiatae* thrive best in a dry, sunny situation. They accordingly constitute an important part of the vegetation of the Mediterranean countries, where these conditions of growth are fulfilled, and where, for example, although not restricted alone to those countries, the officinal Rosemary, Sage, Thyme, and Lavender are found growing wild. Many aromatic species are cultivated as kitchen-herbs: Sweet Marjoram, *Origanum Majorana;* Summer Savory, *Satureia hortensis;* Sweet Basil, *Ocimum Basilicum;* the Garden Thyme, *Thymus vulgaris;* Sage, *Salvia officinalis.*

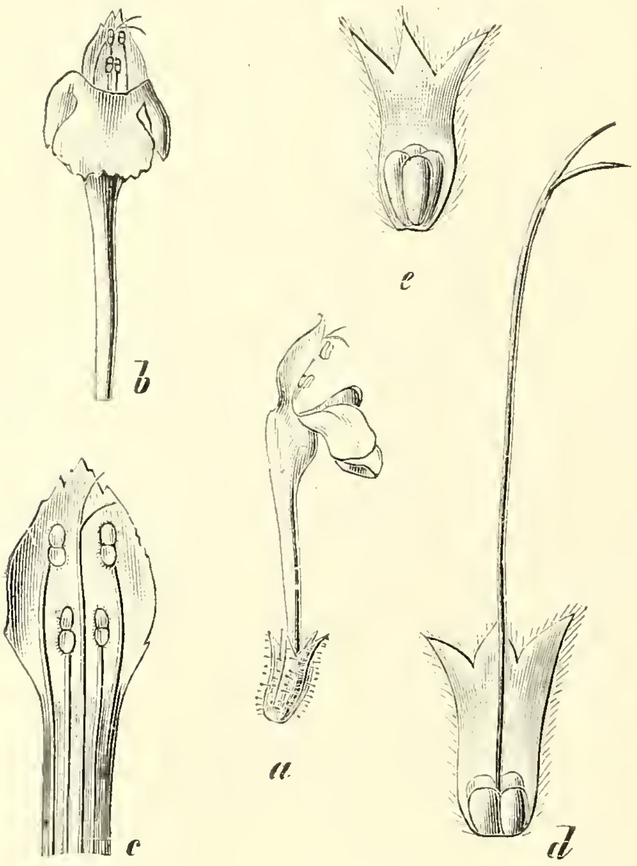


Fig. 659.—*Galeopsis ochroleuca.* *a*, Flower; *b*, the same with calyx removed; *c*, corolla cut open, showing stamens and style; *d*, calyx and gynœcium; *e*, fruit.—OFFICINAL. (*a*, *b*, nat. size; *c*, *d*, *e* × 2.)

Officinal.—*Lavandula vera* yields FLORES LAVANDULAE and OLEUM LAVANDULAE; *Salvia officinalis*, FOLIA SALVIAE; *Melissa officinalis*, the Common Balm (Fig. 658), FOLIA MELISSAE; *Thymus Serpyllum*, HERBA SERPYLLI; *Thymus vulgaris*, HERBA ET OLEUM THYMI; *Rosmarinus officinalis*, FOLIA ET OLEUM ROSMARINI; *Mentha piperita* (Peppermint) (Fig. 657), FOLIA ET OLEUM MENTHAE PIPERITAE and MENTHOLUM; *Mentha crispa*, FOLIA MENTHAE CRISPAE; *Galeopsis ochroleuca*, HERBA GALEOPSIDIS; *Origanum vulgare*, HERBA ORIGANI; *O. majoranae*, HERBA MAJORANAE.

Family **Verbenaceae**.—Ovary one- to two-locular, more usually subdivided and four-chambered (not lobed), the style therefore TERMINAL. Fruit a DRUPE, less frequently a capsule or schizocarp (Fig. 655).

Verbena officinalis.—*Tectona grandis*, an East Indian tree, provides a timber valuable in shipbuilding, Teak. *Verbena Aubletia* is cultivated.

Order 8. Rubiinae

Flowers EPIGYNOUS, actinomorphic or zygomorphic, with the formula Kn, Cn, An, ($G_{\overline{2-3}}$), in which n = 4 or 5. CALYX GREATLY REDUCED; androecium inserted on the corolla; OVARY TWO- to THREE-LOCULAR. Leaves generally OPPOSITE.

FIG. 660.—*Cinchona succirubra* (nat. size).—*OFFICINAL.* (After SCHUMANN and ARTHUR MEYER.)

The *Rubiinae* comprise herbaceous, shrubby, and, more rarely, arborescent plants, varying greatly in general appearance, and, with the exception of opposite leaves, having but little in common in their vegetative structure. The flowers are usually small and aggregated in profusely branched inflorescences, which often assume an umbellate character. The corolla is sometimes campanulate or cylindrical, but, most frequently, rotate or funnel-shaped, according as its lower portion forms a longer or shorter tube. The fruit assumes various forms, sometimes dry, sometimes juicy.

FIG. 661.—*Cephaëlis Ipecacuanha*.—OFFICINAL. (After BERG and SCHMIDT.)

Family **Rubiaceae**.—Flowers ACTINOMORPHIC, andrœcium with FULL NUMBER OF STAMENS; ovary DIMEROUS, BOTH LOCULI fertile. Herbs and woody plants with simple, STIPULATE leaves (Figs. 660-664).

The *Rubiaceae* form one of the largest and most varied families of the vegetable world. The almost always entire and opposite leaves and the invariable presence of stipules, either leafy or scale-like, constitute the characteristics most distinctive of this family. The characteristics given for the order hold good as regards the structure of the fruit and flowers.

SUB-FAMILIES AND REPRESENTATIVE GENERA.—(1) *Stellatae.* Stipules like the leaves; loculi one-seeded: *Galium* (Bedstraw, Cleavers), corolla rotate; *Asperula* (*A. odorata*, Woodruff, Fig. 662), corolla funnel-shaped; *Sherardia* (*S. arvensis*, Field Madder). (2) *Coffeoideae.* Stipules scaly; loculi one-seeded: *Coffea*; *Cephaëlis.* (3) *Cinchonoideae.* Stipules scaly; loculi many-seeded: *Cinchona*; *Uncaria.*

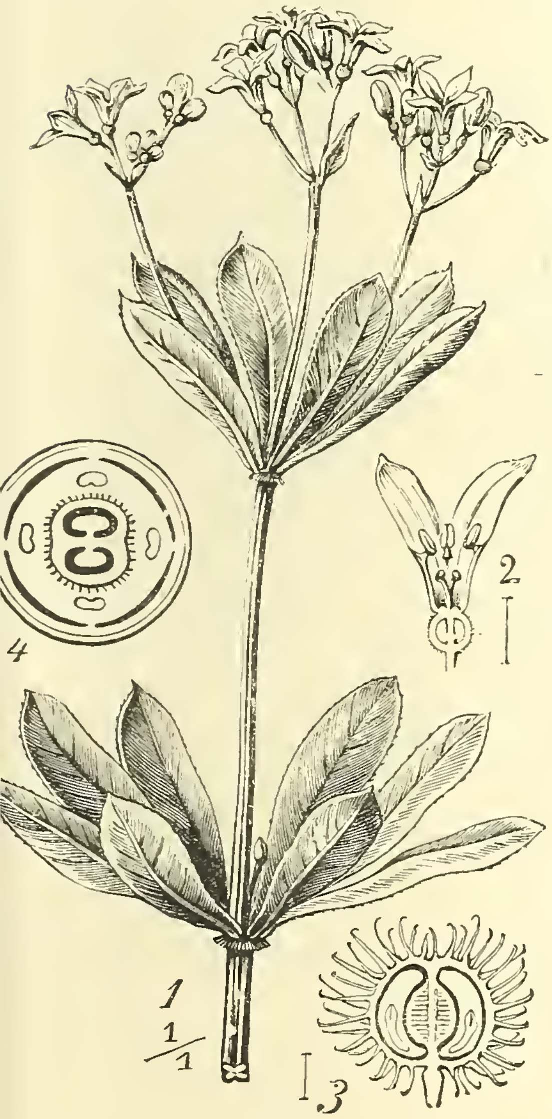


FIG. 662.—*Asperula odorata.* 1, Apex of flowering shoot. The false whorls consisting of two leaves and four to six stipules; 2, flower cut through longitudinally; 3, longitudinal section of fruit; 4, floral diagram. (After WOSSIDLO.)

FIG. 663.—*Coffea arabica.* 1, Flowering branch; 2, fruit; 3, fruit in transverse section; 4, seeds.—OFFICINAL. (After WOSSIDLO.)

GEOGRAPHICAL DISTRIBUTION.—The *Rubiaceae* comprise numerous species of mostly tropical herbs and shrubs. The Coffee-plant, *Coffea arabica* (Fig. 663), is a small evergreen tree, indigenous to the tropical mountainous districts of Eastern Africa, but now cultivated in all warm countries. The white flowers disposed in axillary clusters produce red, cherry-like drupes, each containing two seeds or coffee-beans. Brazil supplies the largest part of all the coffee consumed, but the best comes from South-Western Arabia (Mocha), the Sunda Islands (Java, Celebes), and Ceylon. The various species of *Gardenia* cultivated as ornamental plants also belong to this family.

Officinal.—*Cinchona succirubra* (Fig. 660), *C. Ledgeriana*, and other species of the same genus (Fig. 664) yield the cinchona-bark, Cortex Cinchonae, from which Quinine is prepared. The Cinchonas grow wild in the Andes mountains and are largely cultivated in the mountainous regions of India. They are ever-green trees with lanceolate or roundish leaves and with flowers in pyramid-shaped panicles. The flowers are about 1 cm. long and have a yellowish or carmine-coloured, funnel-shaped corolla with five fringed lobes. When the fruit is ripe the two carpels separate at the base, but are held together at their apices by the calyx; they open by a slit in the middle of the partition dissepiment. *Cephaëlis Ipecacuanha* (Fig. 661), a small under-shrub native of Brazil, yields Radix Ipecacuanhae. *Uncaria Gambir*, an East Indian liane climbing by means of hooks, yields the leaves and young shoots from which Catechu or Gambir is extracted. The alkaloid Coffeïnum is derived from the coffee-bean.

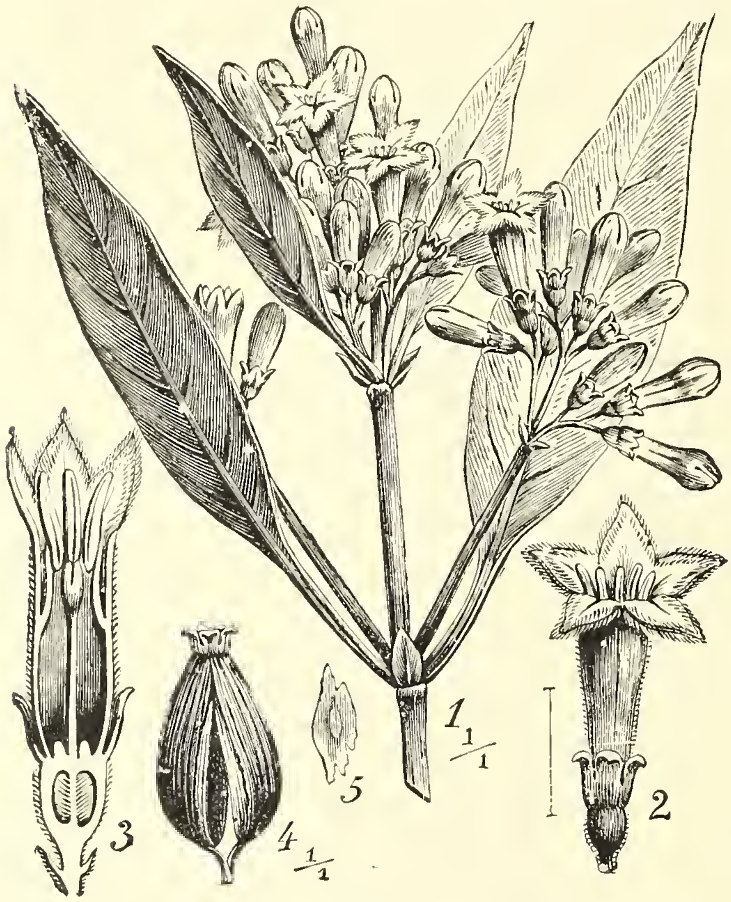


Fig. 664.—*Cinchona lancifolia*. 1, Flowering branch; 2, flower; 3, flower cut through longitudinally; 4, fruit; 5, seed.—*Officinal*. (After Wossidlo.)

Family **Caprifoliaceae.**—Flowers actinomorphic or zygomorphic; andrœcium with full number of stamens; gynœcium usually trimerous; loculi all fertile; mostly woody plants, as a rule with ex-stipulate leaves (Fig. 665).

There is, properly speaking, no characteristic feature which separates the *Caprifoliaceae* and *Rubiaceae*.

The majority of the members of this family are shrubs with simple or pinnate leaves and, most often, with cymose inflorescences. The corolla is rotate, campanulate or tubular, in the last case zygomorphic. The fruit is commonly a berry or drupe.

Subdivisions.—(1) *Sambuceae*. Corolla actinomorphic, rotate; style short; fruit a drupe. *Sambucus*, the Elder, has pinnate leaves and a drupaceous fruit with three stones. The leaves of *Viburnum* (Arrow-wood, Guelder-rose) are simple; the drupes have only one stone. (2) *Lonicereae*. Flowers with an actinomorphic or zygomorphic, tubular corolla and a correspondingly long style, *e.g.* *Lonicera* (Honeysuckle) with zygomorphic flowers, *Linnaea* (Twin-flower), etc.

Geographical Distribution.—The *Caprifoliaceae* are in large part represented by shrubs and small trees growing in woods and thickets in the Temperate Zone of the Northern Hemisphere. Several well-known ornamental plants are included in this family: the Snowball-tree or Guelder-rose, a variety of *Viburnum Opulus*, with sterile flowers only; and the various species of Honeysuckle (*Lonicera*) and Bush-Honeysuckle or *Weigelia*.

OFFICINAL.—*Sambucus nigra* (Fig. 665) yields FLORES SAMBUCI.

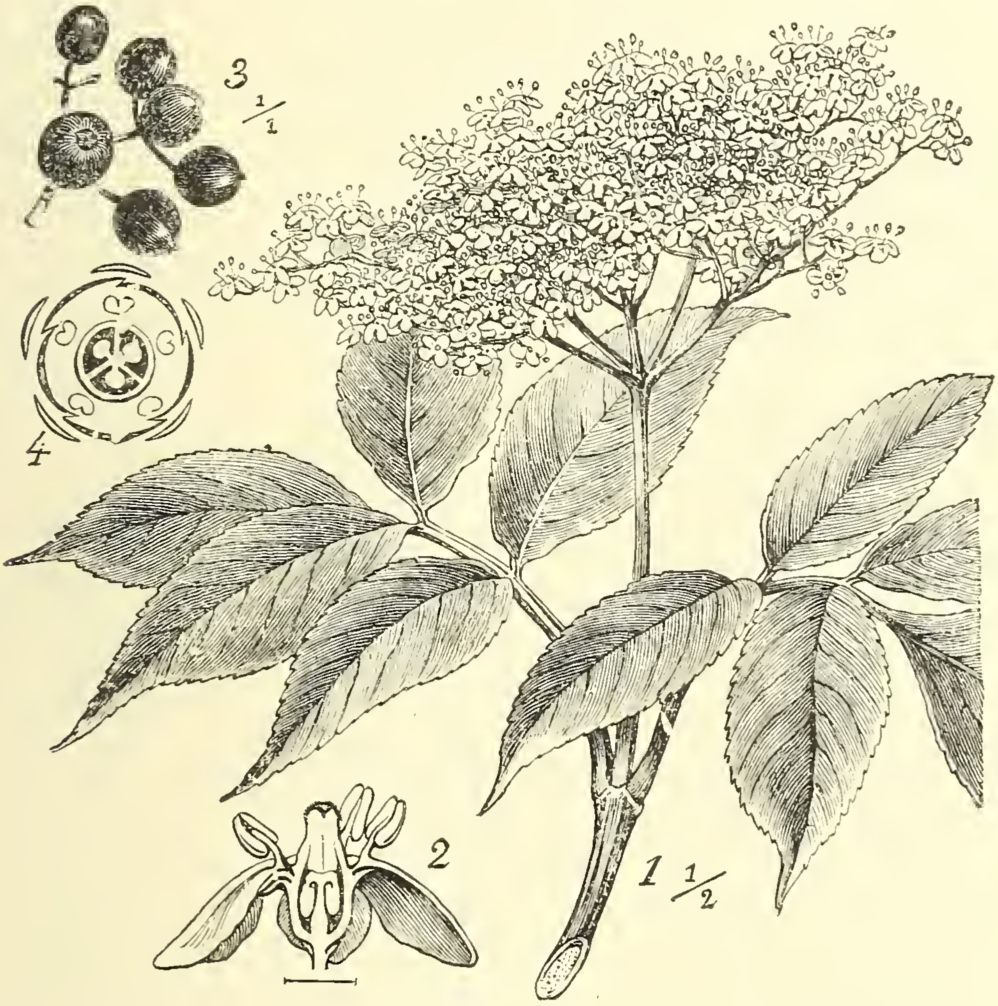


FIG. 665.—*Sambucus nigra*. 1, Flowering branch; 2, a flower cut through longitudinally; 3, fruit; 4, floral diagram.—*OFFICINAL*. (After WOSSIDLO.)

Family **Valerianaceae.**—Flowers ASYMMETRICAL, with pentamerous perianth; andrœcium REDUCED; ovary trilocular, with only one fertile loculus (Figs. 666, 667).

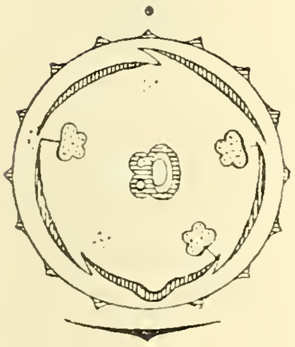


FIG. 666.—*Valeriana*. Floral diagram.

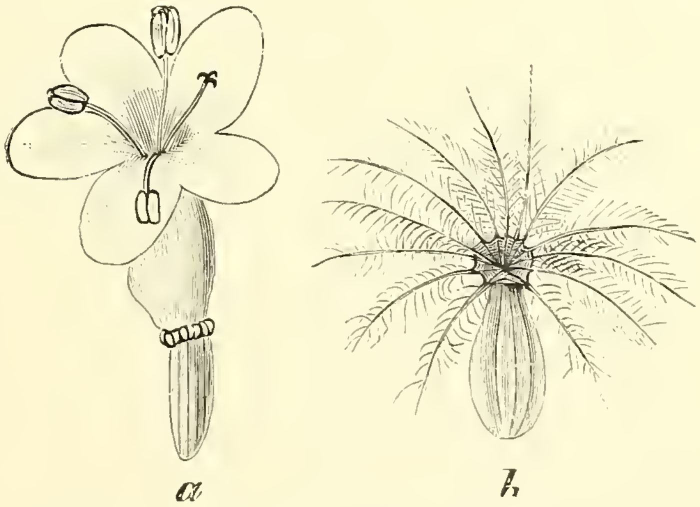


FIG. 667.—*Valeriana officinalis*. *a*, Flower (× 8); *b*, fruit (× 4).—*OFFICINAL*.

The family comprises herbs and small under-shrubs, having simple or pinnate leaves without stipules. The flowers are small and aggregated in profusely branched, dichasial inflorescences. At the time of flowering the calyx is rudimental, but it eventually assumes the form of a feathery pappus (Fig. 667). The actinomorphic or spurred corolla is rotate or funnel-shaped, usually of a light rose-colour. The gynœcium is always asymmetrical, one of the lateral loculi, never the median loculus, being alone fertile (Fig. 666).

Representative Genera. — *Valerianella*, corolla rotate, three stamens. *Valeriana*, corolla funnel-shaped, short-spurred, three stamens. *Centranthus*, corolla funnel-shaped and long-spurred, one stamen.

Officinal. — *Valeriana officinalis* yields Rad. Valerianae and Oleum Valerianae.

Order 9. Campanulinae

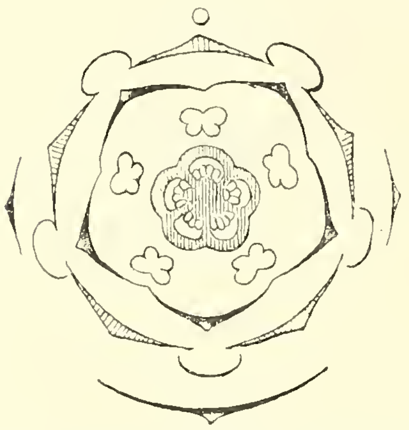


Fig. 668.—Floral diagram of *Campanula medium*. (After Eichler.)

Flowers EPIGYNOUS, actinomorphic or zygomorphic, most frequently with the formula K5, C(5), A5, $G(\overline{2-3})$. Calyx gamosepalous, with long sepals; stamens INSERTED ON THE FLOWER-AXIS, usually with anthers adhering together; ovary TWO- TO THREE-LOCULAR, with numerous ovules. The possession of LATEX is characteristic of most of the plants of this order.

The *Campanulinae* are for the most part herbs with simple, entire, alternate leaves without stipules. Their inflorescences are racemose, either racemes, spikes, or heads. The flowers, which are commonly large and conspicuous, are usually of a blue colour. Except that the corolla is in some instances actinomorphic, in others zygomorphic, the flowers have essentially the same structure throughout the whole order. The anthers, though sometimes free and distinct, more frequently adhere together or are entirely coalescent. The fruit is a capsule, or more rarely a berry.

Family **Campanulaceae.**—Flowers ACTINOMORPHIC; anthers free or adherent; ovary usually TRILOCULAR; fruit a capsule (Figs. 668, 669.)

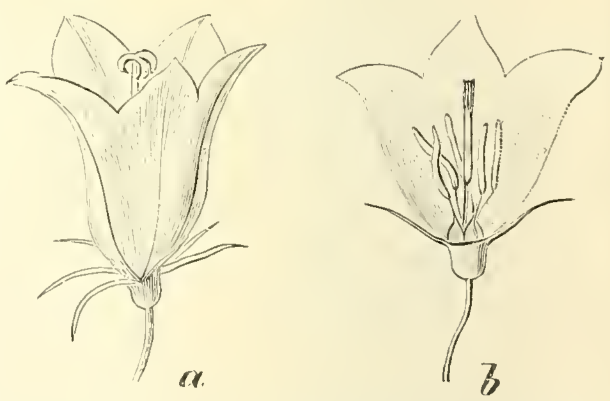


Fig. 669.—*Campanula rotundifolia*. *a*, Flower; *b*, the same cut through longitudinally. (Nat. size.)

Representative Genera.—*Campanula* (Bell-flower), corolla campanulate. *Phyteuma* (Rampion) and *Jasione* (*J. montana*, Sheep's-bit), with flowers having a tubular corolla and aggregated in small heads or spikes. *Specularia* (Venus's Looking-glass), with rotate corolla.

Geographical Distribution.—The members of this family are mostly native of the North Temperate Zone, where they occupy a very prominent position in the vegetation, rather as the result of the striking appearance of their flowers than because of the occurrence of a large number of individuals.

Family **Lobeliaceae.**—Flowers ZYGOMORPHIC. *Lobelia Dortmanna* occur in the ponds of Northern Europe.

Officinal.—Herba Lobeliae is derived from *Lobelia inflata* (Indian Tobacco).

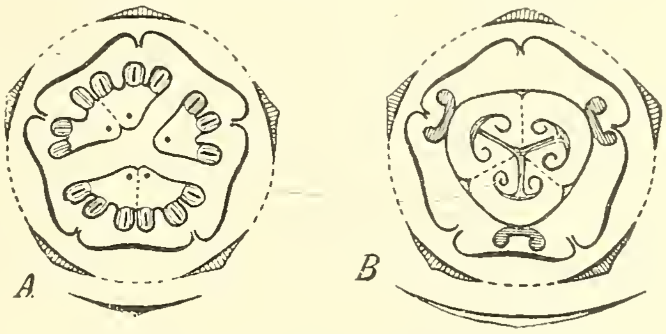


Fig. 670.—*Ecballium* (*Cucurbitaceae*). Diagram of a male (*A*) and of a female flower (*B*). (After Eichler.)

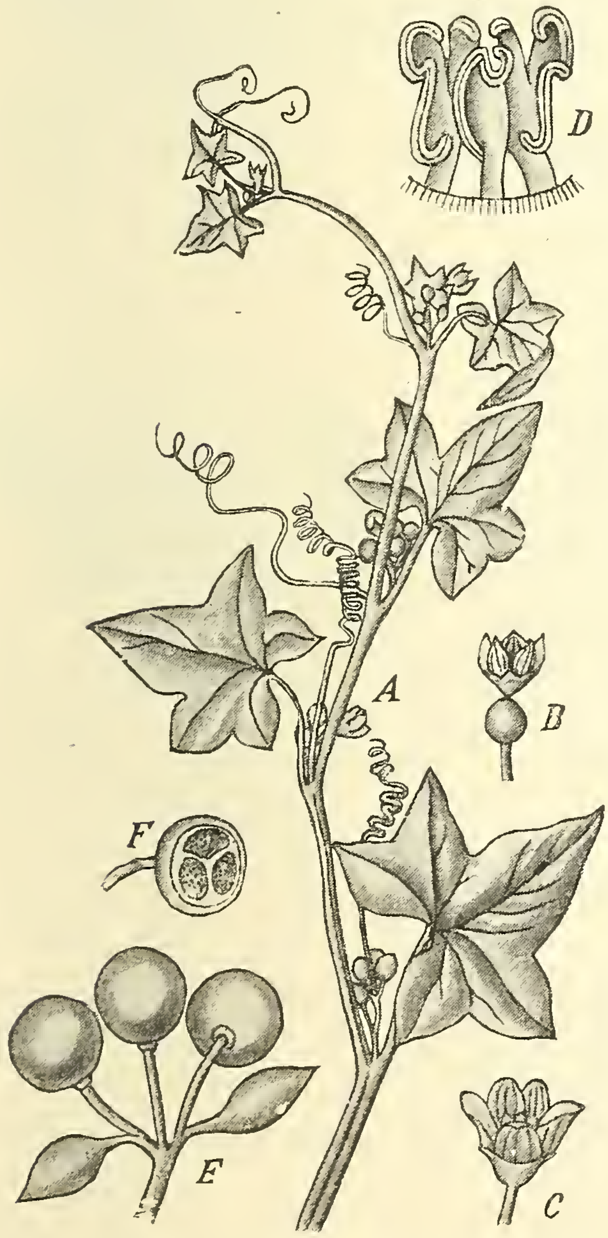


Fig. 671.—*Bryonia dioica*. *A*, Flowering branch (reduced); *B*, female; *C*, male flower (nat. size); *D*, andrœcium (magnified); *E*, fruits; *F*, fruit in section.—*Poisonous*.

Family **Cucurbitaceae.**—Flowers epigynous, UNISEXUAL; calyx and corolla actinomorphic, adnate at the base; stamens five, but they FREQUENTLY COHERE either IN PAIRS, so that there appear to be but three stamens, or, more rarely, they are all united into a column; anthers MONOTHECIOUS; ovary trilocular; fruit baccate, a pepo or succulent berry. Herbs WITHOUT LATEX, commonly climbing by tendrils (Figs. 670-673).

The majority of the *Cucurbitaceae*, although only annual herbs, grow to a large size. They are usually covered with stiff hairs, and have long, often hollow stems with large heart-shaped or lobed leaves and corkscrew-like tendrils arising near the leaves. The flowers are axillary, either solitary or in groups. The corolla and calyx are united together at the base into a cup-shaped receptacle, from the margin of which are given off the narrow sepals. The gamopetalous corolla extends above the level of the cup-shaped receptacle; it is rotate or campanulate, always deeply five-lobed, and of a yellow or whitish colour. The reduction and cohesion of the tortuous anthers (anther-

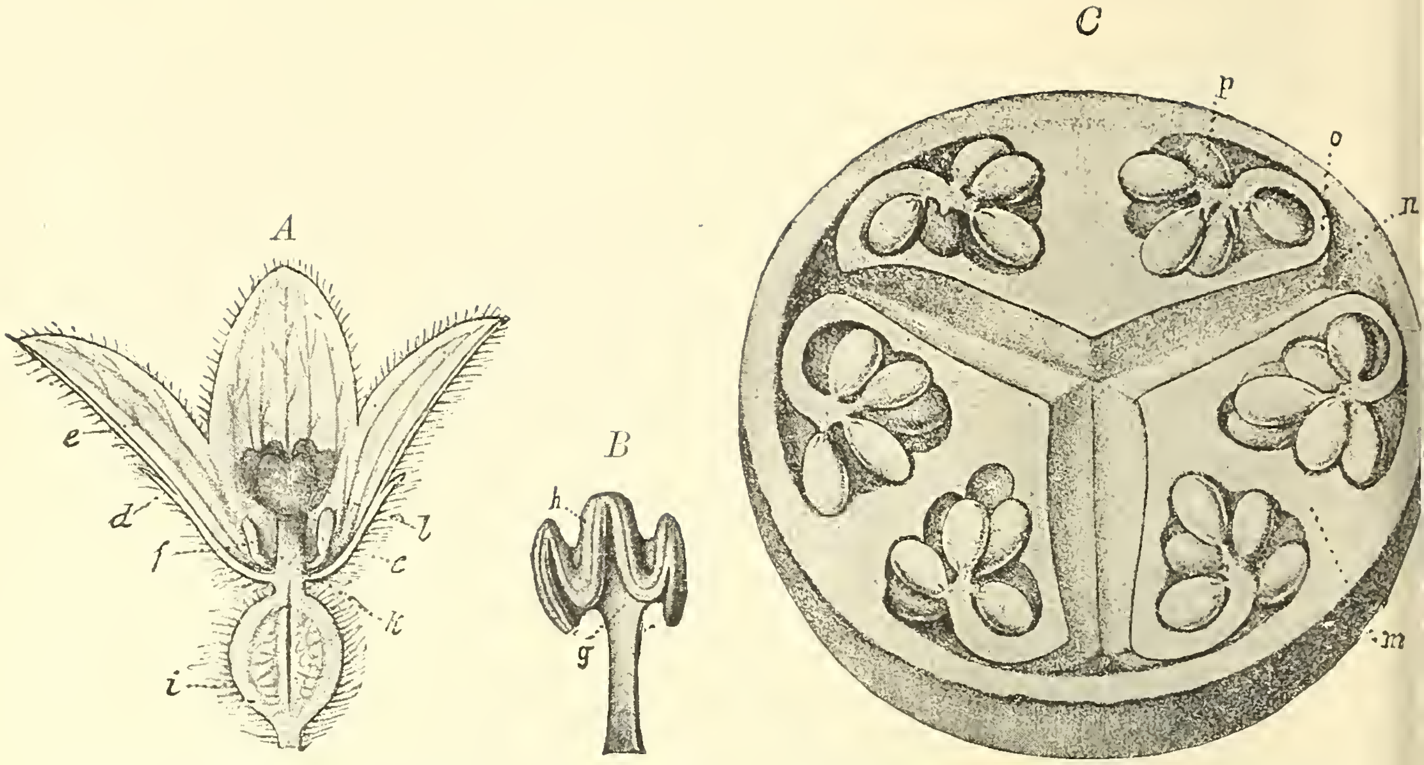


Fig. 672.—*Citrullus colocynthis.* *A*, female flower; *f*, rudiments of stamens; *i*, ovary; *k*, style; *l*, stigma; *c*, calyx-tube; *d*, calyx; *e*, corolla (× 2). *B*, Large stamen; *g*, connective; *h*, anther (× 6). *C*, Fruit cut across. (Nat. size.) (After Berg and Schmidt).

Fig. 673.—*Citrullus colocynthis* (nat. size).—*Officinal.*
(After Berg and Schmidt.)

halves) give the andrœcium a highly characteristic appearance. The three loculi of the ovary are almost completely filled by numerous ovules and projecting fleshy placentæ. The fruit is a spherical or elongated berry, not unfrequently of an enormous size. Its firm, sometimes hard exocarp usually encloses a succulent mesocarp derived chiefly from the placentæ. The seeds are large and flat, and without endosperm.

Geographical Distribution.—The *Cucurbitaceae* comprise for the most part plants of the Tropical Zone, thriving best in the dry open districts. Various species are cultivated for the sake of their fruit, *e.g.* the Pumpkin (*Cucurbita Pepo*), the Cucumber (*Cucumis sativus*), the Musk-melon (*Cucumis Melo*), the Water-melon (*Citrullus vulgaris*), etc.

Poisonous.—*Bryonia dioica* (Fig. 671) and *B. alba*, hirsute tendril-climbers with tuberous roots, lobed leaves, and comparatively small berries, which in the former species are red, in the latter white.

Officinal. — *Citrullus Colocynthis* (Figs. 672, 673), a herb somewhat resembling the Cucumber, native of the African and Arabian deserts, yields Fructus Colocynthidis.

Order 10. Aggregatae

Flowers EPIGYNOUS, actinomorphic or zygomorphic, constructed after the formula K5, C(5), A5, $G\overline{(2)}$; calyx RUDIMENTARY; stamens inserted on the corolla; anthers usually ADHERENT (syngenesious); ovary UNILOCULAR, with one ovule. Fruit indehiscent. Inflorescence a CAPITULUM, surrounded by an INVOLUCRE.

The capitate inflorescence is the most distinctive characteristic of the *Aggregatae.* The margin of the expanded axis of the inflorescence is occupied by numerous hypsophylls, while its whole upper convex or concave surface is thickly beset with small flowers (florets), which are frequently given off from the axils of reduced subtending bracts or scales (paleæ). In its general appearance the whole inflorescence resembles a single flower, particularly when the marginal flowers are larger than the central, and form a sort of corolla about them.

In the united anthers and in the occurrence of septated latex tubes the *Compositae* show a relationship with the *Campanulinae.*

Family **Dipsacaceae.**—Flowers WITH EPICALYX, usually zygomorphic; corolla four- to five-lobed, IMBRICATE IN THE BUD; stamens four, with FREE anthers; style SIMPLE; ovules SUSPENDED; seeds WITH ENDOSPERM. Leaves opposite (Fig. 674).

Herbs with simple or pinnate leaves and many-flowered, flat or convex capitula whose marginal flowers are frequently larger than the central. The possession of an epicalyx consisting of united bracteoles is characteristic of the flowers of this family. The true calyx is rudimental, represented only by teeth or bristles. By the cohesion of the two posterior lobes of the corolla, it frequently becomes apparently tetramerous. The nut-like fruit is enveloped by the persistent epicalyx.

Representative Genera.—(*a*) With paleæ: *Dipsacus* (Teasel), thistle-like with prickly, involucral bracts and scales, corolla four-lobed; *Scabiosa*, involucre herbaceous, corolla five-lobed; *Succisa*, corolla four-lobed. (*b*) Without paleæ: *Knautia*.

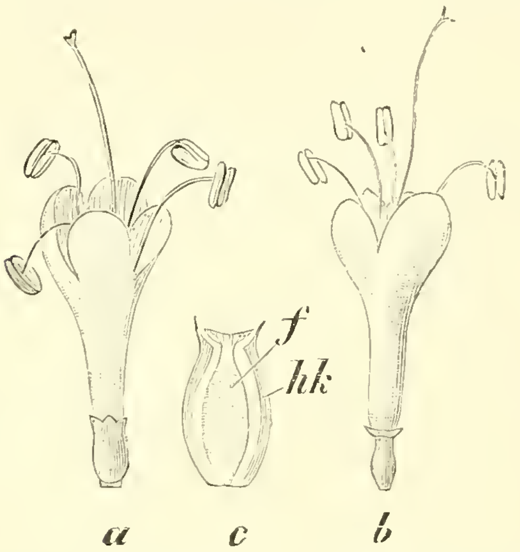


Fig. 674.—*Succisa pratensis*. *a*, Flower with epicalyx: *b*, the same after removal of epicalyx; *c*, fruit in longitudinal section; *f*, ovary; *hk*, epicalyx.

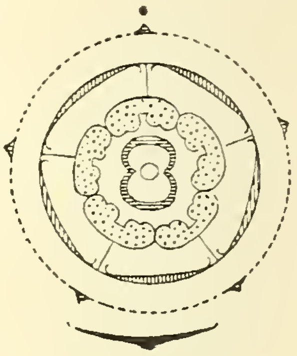


Fig. 675.—*Compositae*. Floral diagram (*Carduus*).

Geographical Distribution.—The *Dipsacaceae* are chiefly met with in sunny situations in the Mediterranean region. Some species occur in more northern latitudes. The heads of *Dipsacus fullonum*, the cultivated Fuller's Teasel, have hooked paleæ, and are used for raising a nap upon woollen cloth.

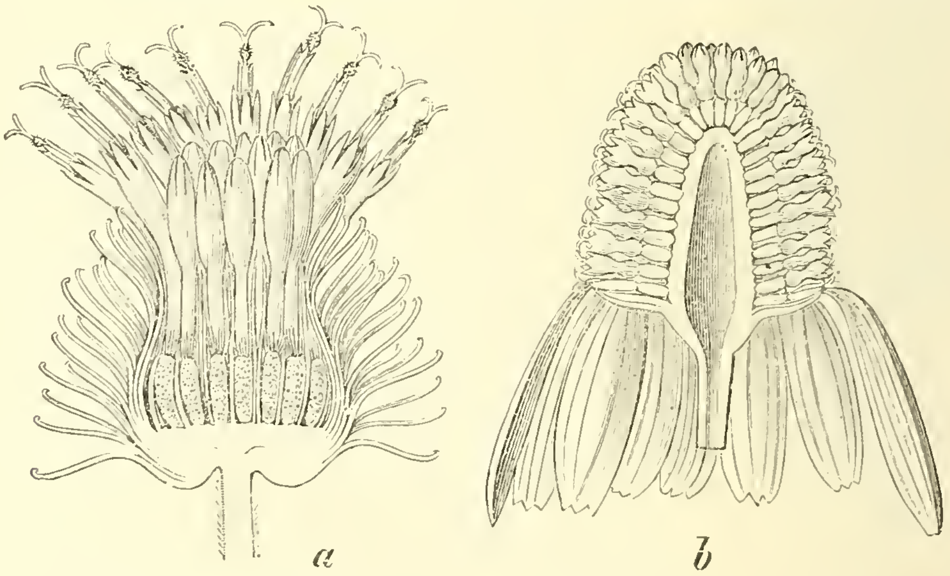


Fig. 676.—Longitudinal section of capitulum, *a*, of *Lappa major* with paleæ; *b*, of *Matricaria Chamomilla* without paleæ.—*Officinal*. (After Berg and Schmidt, magnified.)

Family **Compositae**.—Flowers WITHOUT EPICALYX, actinomorphic or zygomorphic; corolla VALVATE; stamens FIVE, WITH SYNGENESIOUS ANTHERS; style BIFID; ovules ERECT; seeds WITHOUT ENDOSPERM. Leaves commonly alternate (Figs. 675-686).

The *Compositae* comprise mostly herbs, rarely, and then usually confined to the Tropics, shrubs, lianes, and trees. The vegetative organs vary so greatly in their external appearance that they furnish no features that are valuable as a means of distinguishing the family; chemically, however, the *Compositae* are characterised by the presence of inulin in their subterranean parts. The flowers and inflorescences, on the other hand, although they also exhibit great diversity of form, are always easily recognisable. The heads (Fig. 676) are either solitary or combined in compound inflorescences, generally of a dichasial character. The involucral bracts are sometimes herbaceous and green; sometimes scarious and then often highly coloured, as in *Helichrysum* and other genera; sometimes, as in many species of *Centaurea*, they are provided with dry fringed margins, or, as in the Thistle, they may be prickly. The expanded floral axis, the receptacle of the capitulum, is concave or flat (Fig. 676, *a*), slightly elevated or prolonged conically (Fig. 676, *b*). It is sometimes naked (Fig. 676, *b*) or hairy (Fig. 679, *a*), sometimes covered with small scales (Fig. 676, *a*), always pitted like the surface of a thimble, with alveoli in which the separate flowers are inserted (Fig. 679, *a*). The calyx is never

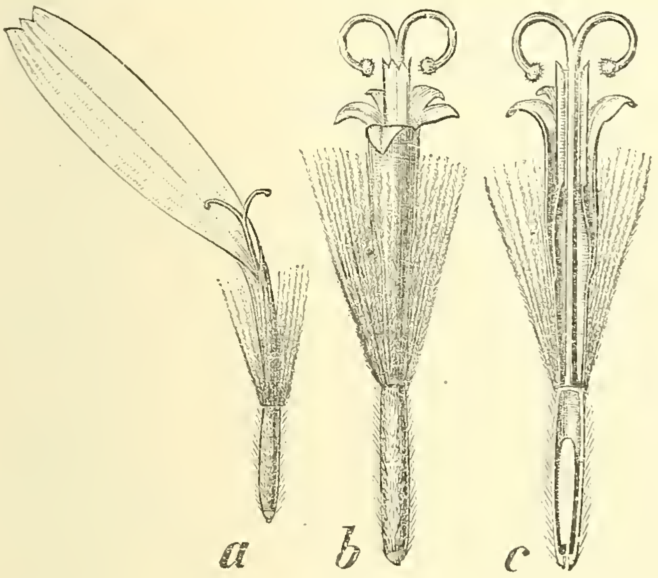


FIG. 677.—*Arnica montana*. *a*, Ray-flower; *b*, disc-flower; *c*, the same cut through longitudinally. (After BERG and SCHMIDT, magnified.)

FIG. 678.—Andrœcium of *Carduus crispus* (×10). (After BAILLON.)

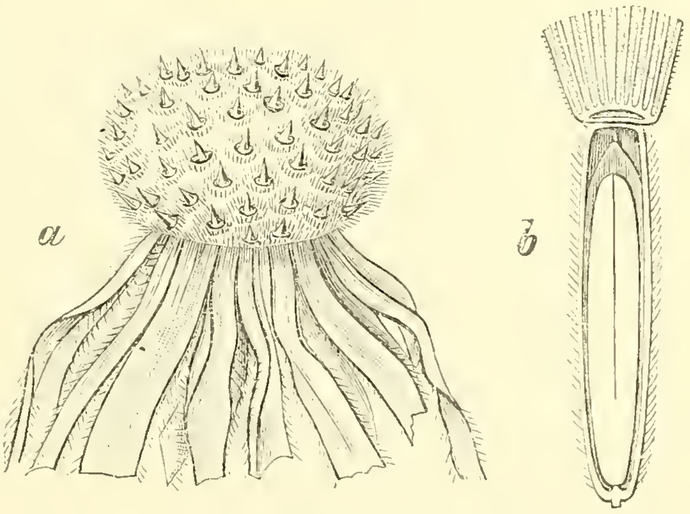


FIG. 679.—*Arnica montana*. *a*, Receptacle of capitulum after removal of fruit; *b*, fruit in longitudinal section, the pappus only partly shown. (After BERG and SCHMIDT, magnified.)

green, and is only rarely represented by five colourless segments. It usually consists of a cushion-like ring which bears the PAPPUS,

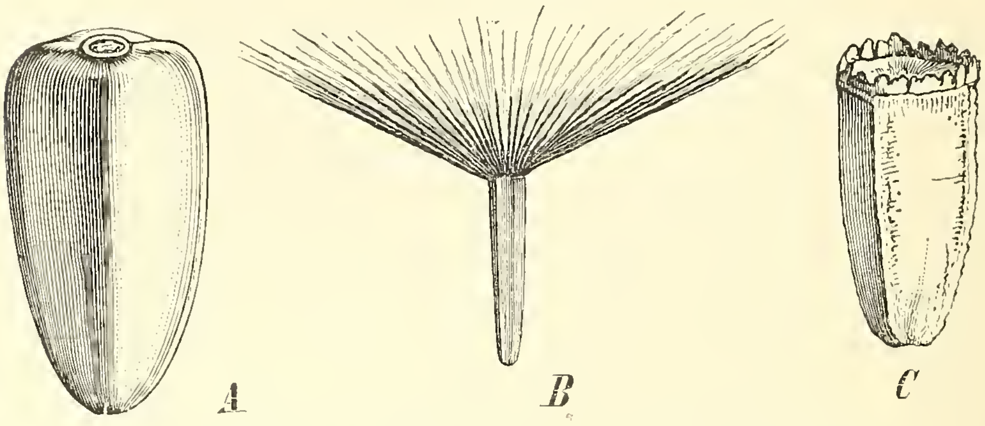


FIG. 680.—Fruits of, *A, Helianthus annuus ; B, Hieracium virosum ; C, Cichorium Intybus.* (After BAILLON.)

FIG. 681.—*Tussilago Farfara.—OFFICINAL.* (After BAILLON.)

FIG. 682.—*Artemisia Cina.* — *OFFICINAL.* (After SCHUMANN and ARTHUR MEYER.)

a tuft of bristles or hairs (Fig. 677). The COROLLA is often regular and five-lobed (Fig. 677, *b*), as in the Thistle. When zygomorphic, it may be BILABIATE, as in the South American *Mutisieae*; more frequently, by the suppression of the upper lip, it becomes ONE-LIPPED or FALSELY LIGULATE (Fig. 677, *a*), as in the marginal flowers of the *Chrysanthemum*; or it is LIGULATE and split for a considerable distance on one side, as in *Taraxacum* (Fig. 686, 2). The one-lipped and ligulate flowers are very similar in appearance, but in the one-lipped flowers the corolla has only three teeth, in the ligulate five. The margin of the receptacle is frequently occupied by one-lipped flowers, and the central portion or disc by actinomorphic tubular flowers. In such cases it is customary to distinguish between RAY-FLOWERS and DISC-FLOWERS. The former are frequently female (*Arnica*, *Inula*, *Matricaria*) or neuter (*Centaurea Cyanus*); the disc-flowers are sometimes all male (*Tussilago*). The STYLE divides at the apex into two variously shaped stigmas, and is

FIG. 683.—*Cnicus benedictus*.—OFFICINAL. (After BAILLON.)

surrounded at the base by a honey-secreting disc. The FRUIT (Fig. 680) is a one-seeded indehiscent fruit or achene; it is usually crowned by a pappus which is of service in the dissemination of the seeds by the wind. The pericarp is leathery, and often adherent to the oily seed.

SUB-FAMILIES, TRIBES, AND REPRESENTATIVE GENERA.—(1) *Tubuliflorae.*

FIG. 684.—*Arnica montana.*—*OFFICINAL.* ½ nat. size. (After BERG and SCHMIDT.)

Flowers actinomorphic or the ray-flowers one-lipped, no latex. (*A*) *Cynareae.* Receptacle with setaceous paleæ, involucral leaves either prickly or with membranaceous margins, style swollen below the stigmas into a cushion-like ring, fruit with pappus. *Carduus* (Plumeless Thistle), involucre prickly, hairs of pappus naked; *Cirsium* (Common or Plumed Thistle), like the preceding, but with feathery pappus; *Cnicus* (Blessed Thistle); *Lappa* (Burdock), tips of involucral leaves hooked ; *Centaurea*, involucral leaves with bristles or membranous margins, ray-flowers, neuter. (*B*) *Eupatorieae*. Flowers actinomorphic, involucre herbaceous, receptacle without paleæ, style not swollen below the stigmas ; *Petasites* (*P. vulgaris*, the Butter-bur) ; *Tussilago* (Coltsfoot) ; *Eupatorium* (Thoroughwort). (*C*) *Astereae*. Marginal flowers female, usually zygomorphic. (*a*) *Anthemideae*, without pappus ; *Anthemis* (Chamomile) and *Achillea* (Milfoil, Yarrow), with paleæ ; *Matricaria* (Wild Chamomile) and *Chrysanthemum*, without paleæ ; *Artemisia* (Wormwood), with tubular flowers only. (*b*) *Heliantheae ; Helianthus* (Sunflower). (*c*) *Calenduleae ; Calendula* (Marigold). (*d*) *Senecioneae*, pappus hairy ; *Senecio* (Groundsel); *Arnica*. (*e*) *Astereae*, pappus bristle-like, frequently brown ; *Aster ; Solidago* (Golden-rod) ; *Erigeron* (Fleabane) ; *Inula* (Elecampane); *Gnaphalium* (Cudweed) ; *Antennaria* (Everlasting Cat's-foot) and *Helichrysum*, with scarious involucre. (*f*) *Ambrosieae*, anthers free ; *Xanthium* (Cocklebur). (2) *Labiatiflorae*. Flowers bilabiate. The majority of the plants in this group are native of South America ; none occur in Europe. (3) *Liguliflorae*. Flowers ligulate. Mostly herbs with septated latex-tubes. *Taraxacum* (Dandelion), with beaked fruit, pappus of unbranched hairs ; *Lactuca* (Lettuce) ; *Crepis* (Hawk's-beard) ; *Hieracium* (Hawkweed), with brownish pappus of unbranched hairs ; *Sonchus* (Sow-Thistle) ; *Scorzonera* and *Tragopogon* (*T. porrifolius*, Salsify), with feathery pappus ; *Leontodon* (Hawkbit).

GEOGRAPHICAL DISTRIBUTION.—The *Compositae* form the largest family of the vegetable kingdom, comprising from 10,000 to 12,000 species, scattered over the whole world. The following are important on account of their special economic value. *Lactuca sativa* (Lettuce), *Cichorium Endivia* (Endive), *C. Intybus* (Chicory), *Cynara Scolymus* (Artichoke), *Scorzonera hispanica* (Viper's-grass), *Artemisia Dracunculus* (Tarragon). Ornamental plants : *Dahlia variabilis* (Dahlia), various species of *Aster* and *Chrysanthemum*, *Helianthus annuus* (Common Sunflower), *Calendula officinalis* (Pot-Marigold).

FIG. 685.—*Lactuca virosa* (½ nat. size). POISONOUS and OFFICINAL.

POISONOUS.—*Lactuca virosa* (Fig. 685), a tall glabrous herb over 1·50 metre high, with elongated amplexicaul leaves and small yellow-flowered capitula in corymbs. The achenes are black and have a white pappus. The whole plant is abundantly supplied with a white, ill-smelling latex, which, as LACTUCARIUM, is officinal in Austria. The plant is not dangerously poisonous. *Lactuca Scariola* (Prickly Lettuce) resembles the preceding species, but has almost vertical leaves, not horizontal as in *L. virosa*, and brownish achenes ; it is not poisonous.

OFFICINAL.—*Arnica montana* (Fig. 684) yields RADIX ET FLORES ARNICAE ; *Artemisia Absinthium* (Common Wormwood), HERBA ABSINTHII ; *Artemisia* sp.

(from Turkestan), FLORES CINAE and SANTONINUM; *Matricaria Chamomilla*, FLORES ET OLEUM CHAMOMILLAE; *Cnicus benedictus* (Fig. 683) (Southern Europe), HERBA CARDUI BENEDICTI; *Inula Helenium* (Common Elecampane), RADIX INULAE; *Tussilago Farfara* (Fig. 681), FOLIA FARFARAE; *Achillea Millefolium* (Common Yarrow or Milfoil), HERBA MILLEFOLII; *Anthemis nobilis* (Garden Chamomile), FLORES CHAMOMILLAE ROMANAE; *Spilanthes oleracea* (South America), HERBA SPILANTHIS; *Lappa vulgaris*, RADIX BARDANAE; *Anacyclus Pyrethrum* (Southern Europe), RADIX PYRETHRI; *Taraxacum officinalis* (Common Dandelion) (Fig. 686), RADIX ET FOLIA TARAXACI; *Lactuca virosa*, LACTUCARIUM.

FIG. 686.—*Taraxacum officinale.* 1, Two capitula and a leaf; 2, a flower; 3, fruit; 4, receptacle with one fruit.—*OFFICINAL.* (After WOSSIDLO.)

Fossil Angiosperms (35)

The first undoubted Angiosperms appear in the Upper Cretaceous. They are represented by numerous species which, like the recent forms, can be divided into Monocotyledons and Dicotyledons. The most ancient forms are known only as leaves, so that their determination is a matter of difficulty. They agree essentially with living Angiosperms, and since they show no similarities to Gymnosperms or Pteridophytes, do not aid in bridging over the gap between the Angiosperms and these groups.

Of Monocotyledons examples of the *Palmae* are known from the Cretaceous period onwards. The leaves of Dicotyledons from the Cretaceous are doubtfully placed in various orders which contain the more lowly organised types (*Amentaceae*, *Platanaceae*); some are ascribed to *Eucalyptus*, but this is probably an error. The Angiosperms of the Eocene and the Oligocene can be determined with greater certainty; even in Northern Europe representatives of existing tropical and subtropical families occurred, *e.g. Palmae*, *Dracaena*, *Smilax* among Monocotyledons, numerous *Amentaceae* (esp. *Quercus*), *Lauraceae* (*Cinnamonum*, etc.), *Leguminosae* among Dicotyledons.

As the present period is approached the fossil Angiosperms throw even less light on the systematic arrangement of the group. The few genera that have become extinct (e.g. *Dryophyllum*, a supposed ancestral form of the Oaks) are wanting even in the Eocene. From the Miocene onwards the specific forms are in part identical with those now living, and in the Quaternary strata all the remains are of existing species. The general character of the Tertiary flora in Europe was very different from that of the present day. It had the aspect of the flora of a much warmer region, and (as in the case of the Gymnosperms) contained forms which now exist only in distant regions. These questions, however, belong rather to Geographical than to Systematic Botany.

INDEX OF LITERATURE

INTRODUCTION AND MORPHOLOGY

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